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Revision of the genus *Cyrtodactylus* Gray, 1827 (Squamata: Gekkonidae) in Australia

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Abstract

The gekkonid lizard genus *Cyrtodactylus* in Australia is revised based on a combination of morphology and mitochondrial (ND2) sequence data. Previous hypotheses that the Australian populations are assignable to a New Guinea species, *C. louisiadensis*, or to a *Cyrtodactylus louisiadensis* species group defined on shared colour pattern and enlarged subcaudal scales, are rejected. Evidence is provided for the existence of five endemic species in Australia, allopatrically distributed. *Cyrtodactylus tuberculatus* (Lucas & Frost) is formally resurrected for Australian populations in the Cooktown area, from Mt Leswell north to Stanley Island. Four new species are described: *C. mcdonaldi* **sp. nov.** in the south, from the Chillagoe area north to Parrot Creek Falls, *C. hoskini* **sp. nov.** from the Iron Range area, *C. adorus* **sp. nov.** from the Pascoe River drainage, and *C. pronarus* **sp. nov.** from the McIlwraith Range. Concordant genetic and morphological evidence enable the hypothesis that *C. adorus* and *C. pronarus* represent a species pair distinct from the sublineage represented by *C. tuberculatus, C. mcdonaldi* and *C. hoskini*.

Key words: Reptilia, Gekkonidae, *Cyrtodactylus*, Cape York, Australia, new species

Introduction

Cyrtodactylus Gray, 1827, is the largest genus of gekkonid lizards. Like many other large genera, its speciose nature has hindered cladistic analysis of both intrageneric relationships and generic limits. A number of genera or subgenera (*Altigekko* Khan 2003, *Cyrtopodion* Fitzinger 1843, *Geckoella* Gray 1867, *Indogekko* Khan 2003, *Mediodactylus* Szczerbak & Golubev 1977, *Nactus* Kluge 1987, *Siwaligekko* Khan 2003, *Tenuidactylus* Szczerbak & Golubev 1984) have been proposed for species formerly treated as part of *Cyrtodactylus*, but there is ongoing dispute about the limits of many of these (see Krysko *et al*. 2007 for a partial review). Even with the removal of all species that could be considered part of these other taxa, *Cyrtodactylus* still includes 137 species. Well over half of those species (78) have been described since 2000 (Fig. 1), and most descriptions are based on small samples (117 of the 137 species have type series of fewer than ten specimens; 26 were described only from holotypes) from few localities (117 were described from one or two localities). There has been little change over time in the sampling/descriptive approach. When the data are divided into four quartiles (years 1827-72, 1873-1918, 1919-64, 1965-2011), there has been little or no change in the mode (1) and median number (1) of localities, or the modal number of specimens (1 for all quartiles except the third, with mode 2), and only a gradual increase in the median number of types (from 2 in each of the first two quartiles, to 3 in the third, and 5 in the most recent quartile). Small, geographically limited samples diminish the capacity to study morphological variation, both within and between populations, and consequently, there has been a tendency either to assign new specimens or populations to existing species without revision of those species or to describe new taxa by comparison only to the limited type series of previously named taxa. This issue has especially hindered understanding and development of taxonomic knowledge of *Cyrtodactylus* in Australia and adjacent parts of New Guinea.

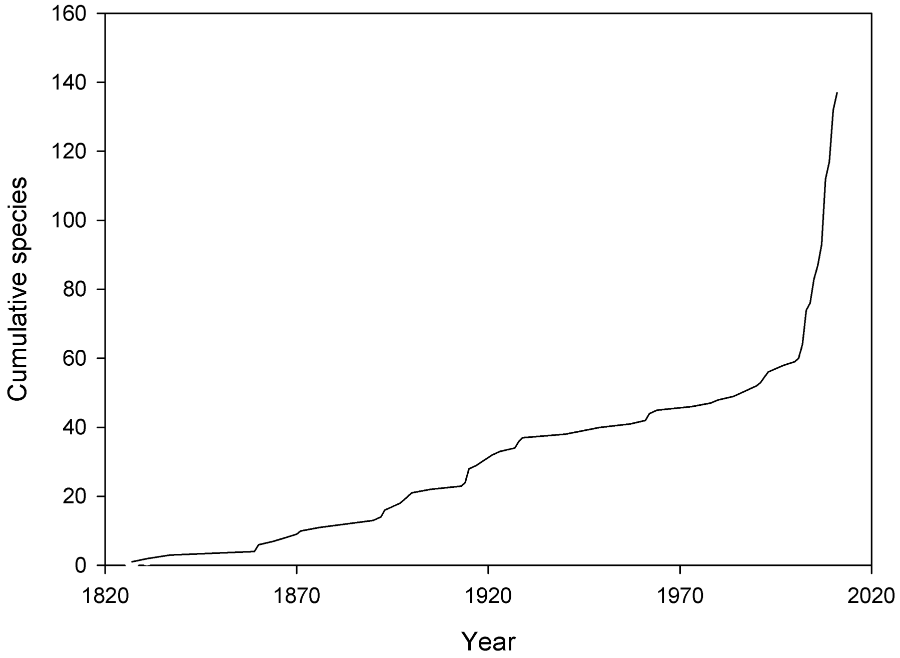

FIGURE 1. Cumulative frequency of descriptions of *Cyrtodactylus* species.

The occurrence of *Cyrtodactylus* in Australia was first formally reported in 1901, with the description of the species *Gymnodactylus olivii* by Garman (1901), based on a single specimen from Cooktown collected by Edmund Abraham Cumberbatch Olive (1844–1921; McKay 2000). The description provided comparison only with *G. pelagicus* (Girard 1858) (now *Nactus pelagicus*). Four years later, Waite (1905) noted the strong similarity of the banded pattern of *G. olivii* with *Gymnodactylus louisiadensis*, described by de Vis (1892) from Tagula Island in the Louisiade Archipelago of New Guinea. Waite did not have access to the type specimen of either species but he did communicate with Olive (though probably Edmund A. C. Olive's son, Edmund Olive, likewise a naturalist) who did not recognise the species amongst the Cooktown fauna he was familiar with. On this basis, together with Waite's identification of a further strongly banded *Cyrtodactylus* specimen from Guadalcanal Island in the Solomon Islands, which he identified as *louisiadensis*, Waite suggested that the type of *olivii* was not Australian but instead came from New Guinea or the Solomon Islands.

Barbour (1921) was the next to consider *C. louisiadensis*. In addition to Waite's Guadalcanal specimen, Barbour reported another specimen of *louisiadensis* from Malaita, thus further confirming the occurrence of the species in the Solomon Islands. Barbour accepted Waite's argument that *G. olivii* was based on a New Guinean specimen but also mentions a specimen from Rockhampton that he referred to *louisiadensis*. Barbour's work was based solely on the Malaita and Rockhampton specimens, together with the holotype of *olivii*. Kinghorn (1928) was able to confirm the existence of banded *Cyrtodactylus* in the Cooktown area, reporting on a specimen sent by Olive to the Australian Museum subsequent to Waite's report. However, he did not examine the holotype, or the material reported by Barbour (1921).

The implication from both Waite and Barbour that *olivii* was New Guinean led to it being treated as a synonym of *louisiadensis* by de Rooij (1915), Kinghorn (1928) and Loveridge (1934), although Zietz (1920), in an uncritical checklist, continued to list *olivii* as a distinct species. Loveridge (1948) referred specimens from Gusiko in Papua New Guinea and New Georgia in the Solomon Islands to *louisiadensis*, supporting the view that *louisiadensis* was a Papuan/Solomon species, but continuing to expand its distribution in the region. This view is understandable; at the time of description of *olivii*, only three species of *Cyrtodactylus* had been described or reported from New Guinea and the Solomon Islands: *novaeguineae* Schlegel 1837[1], *louisiadensis* and *loriae* Boulenger 1898. Both *louisiadensis* and *olivii* had similar strongly banded patterns that were very different to the vertebral blotching present in *novaeguineae* and *loriae*. A further three species of *Cyrtodactylus* were described from New Guinea in the years between 1901 and 1950: *mimikanus* Boulenger 1914, *sermowaiensis* de Rooij 1915 and *papuensis* Brongersma 1934 (originally described as *novaeguineae*, with Brongersma 1928 failing to notice the homonymy). None of these had broad alternating pale and dark bands.

None of the aforementioned authors had noticed the existence of a slightly earlier record of *Cyrtodactylus* in Australia. Lucas and Frost (1900) described *Hoplodactylus tuberculatus* from a single specimen from the Endeavour River, on which Cooktown is located. This species was largely overlooked in subsequent studies, or continued to be listed in its original combination (Zietz 1920; Lucas & le Souef 1909). It was more than 60 years later that Kluge (1963) noted its true generic identity and synonymised the species with *C. louisiadensis*. Based on his examination of the holotype of *tuberculatus* and other (unspecified) Australian specimens, Kluge also viewed the banded *Cyrtodactylus* as a single species, *C. louisiadensis*. He noted slight morphological differences (unspecified) between the Queensland and New Guinean populations and suggested a "moderately long period of isolation from the parental stock".

Lucas and Frost's assignment of *tuberculatus* to a genus otherwise restricted to New Zealand is not as biogeographically anomalous as it appears. At the time of their work, they had recently completed a summary of the New Zealand herpetofauna (Lucas & Frost 1897), and two species of *Hoplodactylus* Fitzinger 1843 were considered to occur in India. Hence, their recognition of a species from Australia was seen as bridging the gap between these two disparate localities. However, one of the two "Indian" *Hoplodactylus*, *H. duvaucelii* (Duméril & Bibron 1836) was later shown (Smith 1933a) to be a New Zealand species with an incorrect type locality. The other, *H. anamallensis* (Günther 1875) was referred to a new genus, *Dravidogekko* by Smith (1933b), which has since been subsumed within the genus *Hemidactylus* Gray 1825 (Bauer & Russell 1995).

Until recent times, *C. louisiadensis* has been treated as a species common to Cape York (Australia), New Guinea and the Solomon Islands (Brown & Parker 1973; Cogger *et al*. 1983). However, Brown and Parker (1973) reported an extraordinarily wide range of enlarged pore-bearing scales in the precloacofemoral region (38-80), noting that "this wide range may reflect population differences, since in our small sample those with the lowest number of pores were from Australia and those with the largest number from the Solomon Islands". Again, Brown and Parker did not identify the specimens they examined to reach this conclusion, other than to note that they had seen few specimens ("several males"). Unfortunately, the number of pore-bearing scales is not useful in assigning the holotypes of *G. olivii* and *H. tuberculatus* to specific populations, as both specimens lack pores and are presumably females (Loveridge 1934; Kluge 1963). Brown and McCoy (1980) considered a new species from Guadalcanal, *C. biordinis*, as part of the "*C. louisiadensis* group" though they did not define that group, other than to include *C. novaeguineae* and *C. loriae* in it. They also provided additional quantification of the variation within a small sample of *C. louisiadensis* (two from the Louisiade Archipelago, four from New Guinea, and 16 from the Solomon Islands) but without any indication of localities within these regions or listing of the specimens examined. They provided no data on pore numbers for the former two regions, suggesting that all those specimens were female.

It was not until 1984 that there was a challenge to a monophyletic or monotypic *C. louisiadensis*. Wells and Wellington (1984, 1985) resurrected *C. tuberculatus* as a distinct Australian species but failed to provide any diagnostic characters, and assigned it to a new genus, *Quantasia*. Only *C. tuberculatus* was formally included in *Quantasia*, which they considered to be restricted to "Cape York Peninsula" (Wells & Wellington 1984). Their generic diagnosis has no description but includes the statement that the genus was distributed in "north eastern Australia, New Guinea and associated islands". Of the morphological characters purported to differentiate the genus, most are widespread in *Cyrtodactylus*, and hence it is not possible to determine the full extent of their genus, although it presumably included *C. louisiadensis*, which was restricted to the type locality, hence leaving other populations in New Guinea and the Solomon Islands innominate. Subsequent authors have failed to recognise *Quantasia*, although some (Bauer 2002, 2003; Batuwita & Bahir 2005; Rösler *et al*. 2007; Rösler & Glaw 2008; Hayden *et al*. 2008) have treated *C. tuberculatus* as distinct, without providing diagnostic characters. Wells (2002) noted that *Quantasia* was intended to encompass the *Cyrtodactylus louisiadensis* group, but did not define the content of that group, and returned *Quantasia* to the synonymy of *Cyrtodactylus*. In the same paper, he provided a redescription of *Cyrtodactylus tuberculatus*, restricting it to the area between the Atherton Tablelands and Cooktown, and described

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1. Most authors (e.g., Brongersma 1934; Wermuth 1965; Bauer & Henle 1994) have given the year 1844 for Schlegel's description, based on the last date in the range given on the cover page of Schlegel's monograph. However, Stejneger (1907) provides evidence that the first 20 pages of text and the first two plates, which include Schlegel's account for *Cyrtodactylus*, were published in 1837 as the first part of the monograph.

a new species, *C. abrae,* nominally from Iron Range. However, the redescription of *C. tuberculatus* was presented without any indication of the author having examined specimens, and gave little detail beyond that already published in general herpetology texts for the genus or the species *C. louisiadensis.* Wells did not specifically cite any sources for his descriptive data, and still did not provide any diagnosis that attempted to explicitly differentiate *C. tuberculatus* from the New Guinean and Solomon Islands populations of *C. louisiadensis*. Further, as noted by Couper *et al*. (2004), the description of *C. abrae* did not meet the requirements of the Code of Zoological Nomenclature as the nominal holotype ("the largest specimen from the type locality [Iron Range] in the Queensland Museum collection") did not exist. At the time of description, there was no indication in any museum collection of a *Cyrtodactylus* population from Iron Range, although the Queensland Museum collection did house specimens from other north Queensland localities (Covacevich & Couper 1991). Despite this, a few authors continued to treat *C. abrae* as a distinct species (Batuwita & Bahir 2005; Hayden *et al*. 2008).

The first explicit hypothesis of relationships was proposed by Kraus and Allison (2006) when they described *Cyrtodactylus murua* (specimens of which had earlier been referred to *C. louisiadensis* by Boulenger 1895) from Woodlark Island. These authors considered that the enlarged subcaudal scales of *C. murua* and *C. louisiadensis*, although apparently convergent with enlarged subcaudal scales in other more geographically distant *Cyrtodactylus*, defined them as "a small clade of taxa related to *C. louisiadensis* that inhabits the eastern Papuan-Solomon Island-Australian region".

Rösler *et al*. (2007) more explicitly used the putative synapomorphy of enlarged subcaudal scales to define a *C. louisiadensis* species group, consisting of *C. louisiadensis*, *C. murua*, *C. tuberculatus* and the newly described *C. salomonensis*, from Ysabel Island, but excluding *C. biordinis*. While the same feature was present in *C. mimikanus* and *C. aaroni* Günther & Rösler 2003 from western New Guinea, those species were excluded from the *C. louisiadensis* group by possession of a larger number of body bands. Hence, the *Cyrtodactylus louisiadensis* group of Rösler *et al*. (2007), Kraus and Allison (2006), and presumably *Quantasia*, differs from that of Brown and McCoy (1980).

Cyrtodactylus tuberculatus was treated as a distinct species by Rösler *et al*. (2007) who redescribed it from three specimens (none of them the types of *tuberculatus* or *olivii*): two females from Cooktown, and one male from 'Australia'. Their comparative material comprised seven specimens from Misima Island that they referred to *C. louisiadensis*, the two types of *C. salomonensis* from a single locality on Santa Isabel Island in the Solomons, and five additional specimens that they tentatively considered close to *C. salomonensis*, three of which came from unknown localities in the Solomons, one from Bougainville Island, and one from an unknown locality in New Guinea. On the basis of this limited sampling, they distinguished the Australian species from other New Guinean and Solomons populations previously ascribed to *C. louisiadensis* by the absence of enlarged tubercles along the lateral skin fold of the trunk. Further, they reported that *C. tuberculatus* had femoral and preanal pore clusters that were separated by several scales lacking pores (an observation based on the single male from an unknown locality). The three specimens examined by these authors had a snout-vent length (SVL) range of 80–89 mm (the type of *tuberculatus* similarly had a reported SVL of 88 mm; Lucas & Frost 1900). This measurement falls well short of the 160 mm SVL reported by Wells (2002) for Australian *Cyrtodactylus* populations.

More recently, Kraus (2008) examined variation in New Guinean populations of banded *Cyrtodactylus,* and divided these populations into five species, *C. epiroticus* (representing populations on the mainland of New Guinea, and possibly Normanby Island), *C. klugei* and *C. lousiadensis* (both restricted to Sudest Island), *C. robustus* (from Rossel Island) and *C. tripartitus* (from Misima Island). Hence, the Misima Island sample that was the basis of Rösler *et al*.'s concept of *C. louisiadensis* did not represent that species. Kraus did not directly examine Australian specimens, relying on the data of Rösler *et al*. (2007) for *C. tuberculatus*. He did not resolve the status of the banded *Cyrtodactylus* of Bougainville Island and other islands in the Solomon group, and did not directly address the hypothesis of Brown and Parker (1973) that *C. louisiadensis* was a single clinally varying species. Although his recognition of five species among the New Guinea populations could be argued to have indirectly refuted this hypothesis, four of the species represent only single small islands, and he did not specifically explore variation among the only wide-ranging taxon, *C. epiroticus*. However, this first extensive sampling of banded *Cyrtodactylus* revealed that these populations did not occur along the south coast of New Guinea. Hence, the concept of a wide-ranging species from the Solomon Islands to Australia required a novel biogeographic pattern amongst Australo-papuan reptiles of an Australian species or population being related to taxa from northern New Guinea and the Solomons, but not southern New Guinea.

In summary, there still remain questions as to whether the Australian *Cyrtodactylus* represent the end of a geographic cline within the species *C. louisiadensis* (as proposed by Brown and Parker 1973, and Brown and McCoy 1980) or whether they are specifically distinct (as proposed by Wells and Wellington 1984, 1985); how many species occur in Australia; and if multiple species do occur in Australia, whether all are specifically distinct from *C. louisiadensis* and the various other species that have been described from that species in New Guinea and the Solomon Islands; and to which taxa the names *C. olivii* and *C. tuberculatus* apply, whether from Australia, New Guinea or the Solomon Islands.

This paper addresses these questions, providing morphological and genetic analyses of geographic variation among banded *Cyrtodactylus* of the region, with particular emphasis on Australian populations.

MATERIALS AND METHODS

Genetics

Sampling strategy. Within Australia, *Cyrtodactylus* tissue samples from twelve Queensland localities were originally available from the Queensland Museum collection. These samples were from the southern end of the Chillagoe–Mungana Caves, north to Stanley Island (in the Flinders Group, off Cape Melville) and to the McIlwraith Range on Cape York Peninsula. The initial trees derived from these samples revealed three major lineages within Australia. We undertook further collecting, emphasising localities intermediate between geographically proximate localities of different lineages, and more extensive sampling from potential localities to the north of the McIlwraith Range. This expanded sampling resulted in additional material from nine new localities including Tozer's Gap (Iron Range National Park) and the Pascoe River area in the far north. For this taxonomic paper, we sequenced 22 *Cyrtodactylus* individuals from 11 Queensland localities, which incorporate most of the currently known Australian distribution (Fig. 2, Table 1).

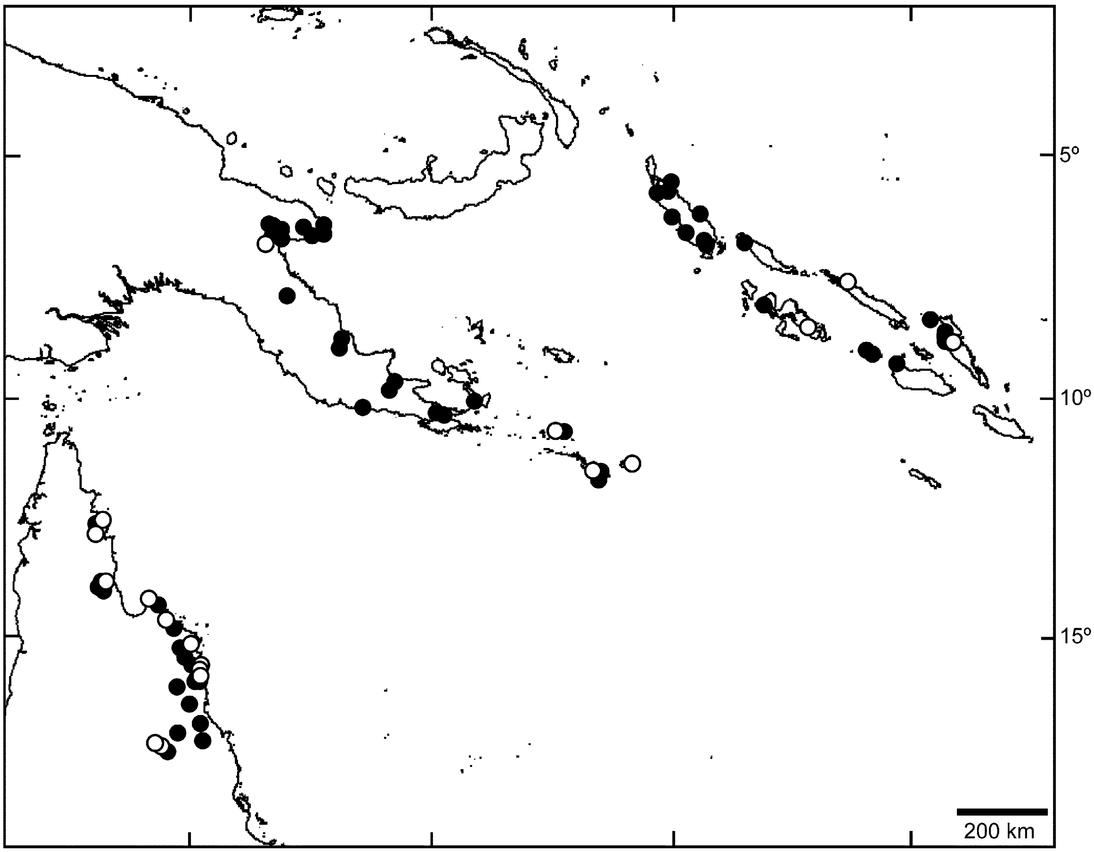

FIGURE 2. Geographic distribution of *Cyrtodactylus* specimens examined in this study. Open symbols represent localities from which genetic samples were obtained.

TABLE 1. *Cyrtodactylus* samples used in phylogenetic analyses.

Species Identification	Sample No	Locality	Museum Registration	QM Tissue Collection	GenBank Accession No	Source
		Australian *Cyrtodactylus*				
C. tuberculatus	2	Black Mountain NP	QM J87009	A004724	HQ401073	This study
			QM J87034	A004743	HQ401074	
C. tuberculatus	1	Cape Melville Campsite	No voucher	A004201	HQ401076	This study
C. tuberculatus	2	Finch Bay, Cooktown	QM J87022	A004732	HQ401084	This study
			QM J87023	A004733	HQ401085	
C. tuberculatus	1	Byer's Creek, Mt Leswell	QM J87031	A004742	HQ401097	This study
C. tuberculatus	1	Mt Webb NP	No voucher	A004247	HQ401099	This study
C. tuberculatus	1	Stanley Island, Flinders Group NP	No voucher	A004241	HQ401109	This study
C. hoskini **sp. nov.**	3	Tozer's Gap, Iron Range NP	QM J86926	A004558	HQ401116	This study
			QM J86927	A004557	HQ401115	
			QM J86950	A004575	HQ401119	
C. mcdonaldi **sp. nov.**	3	Donna Cave	QM J87071	A004778	HQ401129	This study
		The Archways	QM J87075	A004774	HQ401134	
		Royal Arch Tower	QM J87083	A004847	HQ401130	
		(all Chillagoe–Mungana Caves NP)				
C. mcdonaldi **sp. nov.**	2	Parrot Creek Falls	QM J88027	A005337	HQ401150	This study
			QM J88028	A005338	HQ401151	
C. pronarus **sp. nov.**	3	Peach Creek, McIlwraith Ranges	QM J86900	A004540	HQ401161	This study
			QM J86909	A004535	HQ401162	
			QM J86910	A004533	HQ401163	
C. adorus **sp. nov.**	3	Pascoe River	QM J86978	A004599	HQ401165	This study
			QM J86979	A004600	HQ401166	
			QM J86982	A004703	HQ401167	
		PNG, Solomon Islands and SE Asian *Cyrtodactylus*				
C. angularis	1	Muang Sa Kaeo, Thailand	FMNH 265815	N/A	HQ401212	A. Bauer, T. Jackman
C. epiroticus	2	Mt Shungol, MoP, PNG	BPBM 18653	N/A	HQ401195	This study, F. Kraus
			BPBM 18654		HQ401196	
C. jarujini	1	Thaphabat Dist, Lao PDR	FMNH 255472	N/A	HQ401213	A. Bauer, T. Jackman
C. klugei	1	Sudest Island, MBP, PNG	BPBM 19739	N/A	HQ401198	This study, F. Kraus
C. loriae	1	Bunisi Village, MBP, PNG	BPBM 17257	N/A	HQ401209	This study, F. Kraus

…Continue on next page

TABLE 1. (Continued)

Species Identification	Sample No	Locality	Museum Registration	QM Tissue Collection	GenBank Accession No	Source
C. louisiadensis	1	Sudest Island, MBP, PNG	BPBM 19741	N/A	HQ401190	This study, F. Kraus
C. novaeguineae	3	Imonda, WSP, PNG	AM R135520	N/A	N/A	P. Oliver
		Wigote, Torricelli Mtns, WSP, PNG	AM R119547		N/A	
		3.2 km SSE Mt Sapau summit, Torricelli Mtns, WSP, PNG	BPBM 23314		HQ401210	This study
C. robustus	1	Rossel Island, MBP, PNG	BPBM 19727	N/A	HQ401204	This study, F. Kraus
C. salomonensis	1	Malaita Island, Solomon Islands	AM R137204	N/A	HQ401177	This study
C. salomonensis	1	New Georgia Island, Solomon Islands	AM R134930	N/A	HQ401184	This study
C. salomonensis	1	Ysabel Island, Solomon Island	SAM R56879	N/A	HQ401189	P. Oliver
C. sermowaiensis	2	Zfas Village, WSP, PNG	AM R136263		N/A	P. Oliver
		3.2km SSE Mt Sapau Summit, Torricelli Mtns, WSP, PNG	BPBM 23321		HQ401211	This study
C. tripartitus	1	Misima Island, MBP, PNG	BPBM 16864	N/A	HQ401203	This study, F. Kraus
C. zugi	2	Yakut Camp, Batanta Island, Indonesia	MZB lace 5574–5575	N/A	N/A	P. Oliver

Locality Abbreviations
NP = National Park
MBP = Milne Bay Province
MoP = Morobe Province
PNG = Papua New Guinea
WSP = West Sepik Province

Museum Registration Abbreviations
AM: Australian Museum, Sydney, NSW, Australia
BPBM: Bishop Museum, Honolulu, HI, USA
FMNH: Field Museum, Chicago, IL, USA
MZB: Museum Zoologicum Bogoriense, Indonesia
QM: Queensland Museum, Brisbane, QLD, Australia
SAM: South Australian Museum, Adelaide, SA, Australia

For non-Australian populations, we sampled each of the five taxa described or redefined by Kraus (2008), including types of each species (*C. louisiadensis*, n = 1; *C. klugei*, n = 1; *C. robustus*, n = 1; *C. tripartitus*, n = 1; *C. epiroticus*, n = 2). *Cyrtodactylus epiroticus* is the only one of these taxa not confined to a single island and both samples come from the type locality at the western extreme of its distribution (Mt Shungol). From the Solomon Islands, we obtained tissues or were provided with sequence data from three islands: Malaita (n = 1), New Georgia (n = 1) and Ysabel (n = 1, the holotype of *C. salomonensis*) (Fig. 2; Table 2). We also included samples or obtained additional sequences from four other New Guinea and eastern Indonesian species (*C. novaeguineae*, n = 3, *C. loriae*, n = 1, *C. sermowaiensis*, n = 2, *C. zugi*, n = 2) and two more geographically distant species (*C. angularis* (Smith 1921), n = 1) from Thailand and *C. jarujini* Ulber 1993 (n = 1) from Lao People's Democratic Republic. We assumed that the latter two taxa would serve as outgroups. We were unable to obtain tissue samples from two species that had been placed in various previous concepts of a *Cyrtodactylus louisiadensis* group: *C. murua* and *C. biordinis*.

DNA extraction and sequencing. Total genomic DNA was extracted from all tissues using NucleoSpin Tissue Kits (Macherey-Nagel). The entire ND2 gene (approx. 1038bp) was amplified in 2 fragments using the Macey *et al.* (1997) primer L4437 and HCyrlo4980 (5' ATY ATG CGG GTT TGT GTT TGG TT 3', this study) for the first fragment and LCyrlo4876 (5' TCA ACR TGA CAA AAA ATC GC 3', this study) and H5540 (Macey *et al.* 1997) for the second fragment. Each 25 µl reaction contained 1x Taq polymerase buffer with a final concentration of 2.5 mM MgCl2, 0.4 µM each primer; 0.8 mM dNTPs, 1% BSA and 0.65 U of Taq polymerase. The use of the hot start polymerase HotMaster Taq (5 Prime) required an initial denaturation at 94° C for 2 min prior to the commencement of the remaining cycle parameters: 35 cycles of 94° C for 20 sec, 52° C for 20 sec, 65° C for 30 sec and a final extension 65° C for 5 min, 22° C for 10 sec. Amplification conditions and PCR parameters were identical for each fragment.

PCR products were either sequenced directly or gel purified (MoBio UltraClean Gel Spin kit). Sequencing reactions were carried out according to standard ABI PRISM dye-deoxy terminator sequencing protocols using Big Dye Terminator version 1.3. Sequences from the new specimens have been deposited in GenBank nucleotide sequence database (see Table 2 for details of all samples and sequences used in this study including Genbank accession numbers). Chromatographs were checked and all sequences were aligned manually using Se-Al v2.0a10 (Rambaut 1996).

Phylogenetic analyses. Bayesian phylogenetic analyses were carried out in MrBayes v3.1.2 (Ronquist & Huelsenbeck 2003) and posterior probabilities were calculated using a Markov chain, Monte Carlo (MCMC) sampling approach. These analyses used the GTR (general time reversible model) + G (gamma distribution of rates) and I (proportion of invariant sites) model of sequence evolution, as determined by the Akaike and Bayesian information criteria (AIC and BIC) in jModeltest v0.1.1 (Guindon & Gascuel 2003; Posada 2008). By default MrBayes v3.1.2 performs two independent runs. We ran the analysis twice so that four independent runs were performed. For each run, starting trees were random and 4 simultaneous Markov chains were run for 2,000,000 generations with trees sampled every 1000 generations resulting in a total of 8,000 saved trees over the four runs. Burn-in values for each run were set at 100,000 generations (100 trees) after empirical values of stabilizing likelihoods indicated that convergence of the MCMC chains had been reached. A combined majority rule consensus tree from the four independent runs, was generated in PAUP* v4.b.10 (Swofford 2002) by sequentially importing the four MrBayes tree files (.t files); excluding the first 100 trees of each tree file and retaining the previous 1900 trees in memory. The resulting consensus tree was therefore constructed from 7600 trees. The posterior probabilities on the consensus tree are indicated only where branch support is greater than 0.6 (Posada & Crandall 1998).

Morphology

Specimen sources and character definitions. We examined all specimens (n = 274) referred to *Cyrtodactylus louisiadensis* or to species described from within that nominal species in the collections of the Australian Museum, Sydney (AM), Queensland Museum, Brisbane (QM), South Australian Museum, Adelaide (SAM), Museum of Victoria, Melbourne (MV), American Museum of Natural History, New York (AMNH), Bishop Museum, Honolulu (BPBM) (some of which were later deposited in the Papua New Guinea National Museum, Port Moresby (PNGNM)), Museum of Comparative Zoology, Harvard, Cambridge (MCZ), and National Natural History Museum, Smithsonian Institution, Washington (USNM).

TABLE 2. Uncorrected sequence divergence estimates within and between Australian, PNG and Solomon Is. *Cyrtodactylus* species. Values on the diagonal (in bold) are average within species estimates, values below the diagonal are average between species estimates. Standard errors are presented where there are more than two non-identical sequences.

	C. tuberculatus	*C. hoskini*	*C. mcdonaldi*	*C. pronarus*	*C. adorus*	*C. novaeguineae*	*C. zugi*	*C. salomonensis*	*C. louisiadensis*	*C. epiroticus*	*C. tripartitus*	*C. klugei*	*C. robustus*	*C. loriae*	*C. sermowaiensis*	*C. angularis*
C. tuberculatus	**2.03% ±0.01**															
C. hoskini	12.12% ±0.01	**0.00%**														
C. mcdonaldi	11.07% ±0.01	11.79% ±0.02	**5.78% ±0.01**													
C. pronarus	16.81% ±0.01	17.72% ±0.01	16.72% ±0.01	**0.65% ±0.01**												
C. adorus	14.28% ±0.01	16.43% ±0.01	14.54% ±0.01	8.53% ±0.01	**0.00%**											
C. novaeguineae	18.00% ±0.10	17.37% ±0.09	17.18% ±0.08	18.75% ±0.06	17.19% ±0.13	**2.46% ±1.17**										
C. zugi	16.73% ±0.07	17.22% ±0.08	16.46% ±0.25	19.21% ±0.06	18.06% ±0.06	12.92% ±0.12	**0.49%**									
C. salomonensis	19.18% ±0.16	20.02% ±0.38	19.44% ±0.32	23.57% ±0.38	21.44% ±0.47	18.76% ±0.30	19.80% ±0.32	**8.34% ±0.66**								
C. louisiadensis	20.51% ±0.12	20.78% ±0.06	20.12% ±0.08	21.24% ±0.07	19.87% ±0.00	20.31% ±0.36	20.47% ±0.06	15.72% ±0.42	**N/A**							
C. epiroticus	18.85% ±0.09	19.52% ±0.06	19.13% ±0.06	19.82% ±0.10	18.32% ±0.00	19.77% ±0.12	18.64% ±0.08	13.44% ±0.12	10.90% ±0.05	**0.10%**						
C. tripartitus	17.81% ±0.12	19.01% ±0.09	18.90% ±0.18	20.77% ±0.07	19.77% ±0.00	19.51% ±0.33	18.68% ±0.25	14.68% ±0.78	15.99%	14.10% ±0.05	**N/A**					
C. klugei	17.45% ±0.10	18.36% ±0.03	17.62% ±0.32	21.25% ±0.07	19.38% ±0.00	19.78% ±0.04	19.54% ±0.06	16.25% ±0.45	17.05%	15.65% ±0.05	16.38%	**N/A**				
C. robustus	17.57% ±0.16	19.47% ±0.03	18.37% ±0.10	22.20% ±0.08	20.64% ± 0.00	19.92% ±0.11	19.34% ±0.13	16.60% ±0.52	17.44%	15.85% ±0.05	16.38%	12.02%	**N/A**			
C. loriae	20.11% ±0.06	19.97% ±0.05	18.59% ±0.46	22.82% ±0.08	22.00% ±0.00	20.68% ±0.2	19.76% ±0.00	21.38% ±0.97	21.71%	20.25% ±0.00	20.54%	19.28%	20.16%	**N/A**		
C. sermowaiensis	19.05% ±0.07	19.85% ±0.17	18.96% ±0.15	20.61% ±0.09	19.21% ±0.21	19.86% ±0.14	19.81% ±0.16	21.74% ±0.58	22.47% ±0.30	20.17% ±0.05	21.55% ±0.64	18.62% ±0.01	19.70% ±0.03	19.91% ±0.25	**4.54%**	
C. angularis	24.88% ±0.1	25.22% ±0.05	24.21% ±0.29	26.76% ±0.1	24.82% ±0.00	26.32% ±0.23	25.26% ±0.00	24.79% ±0.96	26.17%	25.15% ±0.05	24.91%	23.65%	24.82%	25.11%	25.14% ±0.076	**N/A**
C. jarujini	2305% ± 0.1	25.26% ±0.05	22.89% ±0.24	26.30% ±0.03	24.95% ±0.00	24.80% ±0.13	22.28% ±0.06	25.44% ±1.08	25.13%	24.07% ±0.05	25.36%	23.82%	24.14%	25.87%	23.26% ±0.76	22.39%

TABLE 3. Discriminant function coefficients, standardised by within-variances, for female and male analyses.

	Females				**Males**		
Character	**Function 1**	**Function 2**	**Function 3**	**Function 4**	**Function 1**	**Function 2**	**Function 3**
SVL	0.317	0.150	0.037	0.382	0.436	0.785	0.303
Femoroprecloacal scales	1.060	0.022	0.310	-0.179	1.035	-0.219	-0.173
Transventral scales	0.130	0.184	-0.390	0.471	0.197	-0.183	0.462
Fourth toe lamellae	0.101	-0.741	0.066	0.646	-0.365	0.691	0.213
Dorsal tubercle rows	0.057	-0.491	-0.101	-0.150	0.370	0.449	-0.287
Adjusted AGL	0.083	-0.293	0.036	0.032	0.292	0.232	0.350
Adjusted HLL	-0.010	-0.098	-0.703	0.267	0.213	0.217	0.114
Adjusted TW	0.611	0.311	0.092	-0.225	-0.221	0.426	0.039
Adjusted HW	-0.604	-0.353	-0.093	0.814	-0.112	-0.599	-1.252
Adjusted HD	0.163	-0.216	0.382	0.408	-0.464	0.094	0.324
Adjusted IN	-0.133	-0.594	-0.202	-0.521	-0.074	-0.183	-0.537
Adjusted EN	0.575	-0.224	-0.052	-0.021	0.025	0.598	0.098
Adjusted EE	-0.411	0.832	0.386	0.770	-0.028	-0.110	0.913
Adjusted Ear	-0.091	-0.441	0.165	0.181	-0.327	0.114	0.317

The following morphometric characters were measured, where possible, on each specimen from Australian collections: snout-vent length (SVL), measured along the ventral midline, from the tip of the snout to the anterior margin of the vent, with the specimen straightened against a flat ruler; axilla-groin length (AGL), similarly measured, from the posterior edge of the junction of the brachium and body wall to the anterior edge of the junction of the thigh and body wall, with the limbs held at right angles to the body; tail length (TL), similarly measured, from the anterior margin of the vent to the tip of the tail in individuals with complete original tails only; head length (HL), obliquely from the midline of the tip of the snout to the anterior margin of the ear opening; head width (HW), across the widest point of the head, anterior to the ears; head depth (HD), at the deepest point of the head, over the parietal table, and including the lower jaw; internarial interval (IN), between the medial margins of the nostrils; snout length (SL), from the midline of the tip of the snout to the anterior margin of the bony orbit; eye-naris interval (EN), from the posterior margin of the nostril to the anterior margin of the bony orbit; eye diameter (EYE), from mid anterior to mid posterior margin of spectacle, excluding the peripheral scales; eye-ear interval (EE), from posterior margin of bony orbit to anterior margin of ear; ear diameter (EAR), obliquely across the maximum diameter of the ear; antebrachial length (FLL), with limb strongly flexed, from elbow to distal carpal articulation; tibia length (HLL), with limb strongly flexed, from knee to tarsus; tail width (TW), across base of tail immediately posterior to the postcloacal sacs. SVL, AGL and TL were measured to the nearest 0.5 mm with a steel ruler; the other measurements were taken with dial calipers, viewed under a dissecting microscope, to the nearest 0.1 mm.

The following meristic characters were counted on each individual in Australian collections: number of enlarged scales in a row on the ventral surface of the femoro-precloacal area, counted along the most posterior enlarged row of the femoral area; number of pores along the scales in this row, when present, and the number of scales involved in breaks in the pore-bearing series; longitudinal rows of ventral scales counted transversely across the mid-point of the axilla-groin interval, between ventrolateral skin folds and including the scales to the peak of the fold; number of longitudinal rows of enlarged tubercles across the body dorsum, at the midpoint of the axilla-groin interval; number of supralabial scales, counted from the first scale posterior to the rostral scale, posteriorly to the point at which the scale row tilts dorsally posteroventral to the eye; number of infralabial scales, counted from the first scale posterior to the mental scale, posteriorly to the last enlarged scale. Because the subdigital lamellae show an abrupt change in size below the proximal interphalangeal joint, as the digit arches dorsally, subdigital lamellae on each digit were counted in two series: a basal enlarged series, counts commencing proximally at the first noticeably enlarged scale on the sole of the foot (this scale was either about 50% larger than the granules surrounding it, or was preceded by a pair of smaller scales) and ending at the last enlarged scale before the sharp reduction in lamella width; and a distal narrow series, from the first scale beyond this point, to and including the scale sheathing the claw. This method of counting subdigital lamellae often included some scales on the sole of the foot rather than just those below the phalanges. However, this method was adopted due to the difficulty in determining exactly where to commence counting on the digit, due to the slight webbing at the base of some digits. We counted lamellae on only one foot per specimen; usually the left, unless damage or distortion made it necessary to examine the right foot.

For specimens from institutions outside Australia, we counted and measured a reduced set of characters: SVL, ventral scales and enlarged femoroprecloacal scales and pores, together with the number and configuration of dark bands on body and tail.

Morphological analyses. To test the hypothesis that the Australian *Cyrtodactylus* represent one extremity of a cline of variation in a widespread taxon *C. louisiadensis*, we studied the pattern of geographic variation in femoroprecloacal pores within *C. louisiadensis* sensu lato. The distribution of this broader entity was represented by three arcs running from north-west to south-east: the northernmost from Bougainville to the Solomon Islands (5º S 154º E to 9º S 160º E), the second along the northern New Guinea coast, and south-east through the Louisiade Archipelago (6º S 146º E to 11º S 154º E), and the southernmost along the north-east Australian coast and ranges (12º S 143º E to 17º S 145º E) (Fig. 2). We plotted femoroprecloacal pore number in each arc against longitude for the two northern arcs (as the range of longitude was greater than for latitude in both, and longitude and latitude were correlated) and against latitude for the Australian arc, to explore the nature of the relationship and regressed pore count against the same variables with simple linear regression. As two populations (in the south in Australia, and on Misima Island in New Guinea) had gaps in the femoroprecloacal pores series, and as pores were only present in males, we also considered the pattern of variation in each arc for total number of enlarged femoroprecloacal scales (allowing us to exclude the gaps, and increase the samples by inclusion of females), and for number of transventral scales, which should also be affected in the same way in each arc if a general cline existed from high numbers of less enlarged scales in the north to small numbers of more enlarged scales in the south.

TABLE 4. Allometric equations and calculated values for cranial and somatic proportions in *Cyrtodactylus tuberculatus*. Values a and b solve the equation $y = bx^a$, r = correlation coefficient, se = standard error of a, Allom = direction of allometry, C_{46}, C_{90} and C_{120} are calculated percentage proportions (y/x) at SVL = 46, 90 and 120 mm (minimum, minimum mature and maximum size).

y	x	a	b	r	se	Allom	C_{46}	C_{90}	C_{120}
AGL	SVL	1.144	0.2214	0.973	0.035	+	38.4	42.3	44.1
TW	SVL	1.216	0.0311	0.914	0.069	+	7.1	8.2	8.7
FLL	SVL	1.073	0.1105	0.984	0.025	+	14.6	15.3	15.7
HLL	SVL	1.071	0.1309	0.985	0.024	+	17.2	18.0	18.4
HL	SVL	0.869	0.5310	0.968	0.029	-	32.2	29.5	28.4
HW	HL	0.956	0.869	0.934	0.047	0	77.2	75.2	74.4
HD	HL	0.836	0.7283	0.864	0.062	-	46.8	42.5	40.8
SL	HL	0.910	0.5299	0.965	0.032	-	41.6	39.5	38.6
EN	HL	0.941	0.3559	0.958	0.036	0	30.4	29.3	28.9
Eye	HL	0.743	0.5347	0.926	0.039	-	26.8	23.0	21.6
EE	HL	1.033	0.2717	0.941	0.048	0	29.7	30.3	30.5
Ear	HL	1.060	0.0784	0.859	0.081	0	9.2	9.6	9.7
IN	HL	0.732	0.330	0.900	0.046	-	16.0	13.7	12.8

In order to test whether the five geographically discrete genetic lineages in Australia were distinguishable morphologically from each other, we used discriminant function analyses.

For these discriminant function analyses, for morphometric characters, we first tested for the existence of significant sexual dimorphism within the lineage with the largest sample numbers (the lineage centred over the Cooktown region) using analysis of covariance of natural logarithm-transformed values, with ln(SVL) as the independent variable for body, tail and limb measurements and head length, and ln(HL) as the independent variable for other head measurements. Most proportions showed significant sexual dimorphism (Table 5).

TABLE 5. Sexual dimorphism in cranial and somatic proportions in *Cyrtodactylus tuberculatus*. Tests of significance (i) and allometric and calculated values for males and females in sexually dimorphic characters (ii). Values a and b solve the equation $y = bx^a$, r = correlation coefficient, se = standard error of a, C_{90} and C_{117} are calculated proportions at SVL = 90 and 117 mm (minimum mature and maximum male SVL). The measurements for HL as an independent variable at these sizes are from the relationship between HL and SVL, which is not sexually dimorphic. Boldened values are statistically significant ($P < 0.05$).

(i)

		slopes			**intercepts**		
y	**x**	**F**	**d.f.**	**P**	**F**	**d.f.**	**P**
AGL	SVL	3.318	1,59	0.074	6.177	1,60	**0.016***
TW	SVL	1.165	1,58	0.285	4.388	1,59	**0.041***
FLL	SVL	0.071	1,58	0.791	8.129	1,59	**0.006****
HLL	SVL	1.510	1,59	0.224	14.940	1,60	**<0.001*****
HL	SVL	1.084	1,58	0.302	1.192	1,59	0.279
HW	HL	6.328	1,58	**0.015***			
HD	HL	3.043	1,58	0.086	0.695	1,59	0.408
SL	HL	6.535	1,58	**0.013***			
EN	HL	10.497	1,58	**0.002****			
Eye	HL	0.541	1,58	0.465	2.540	1,59	0.116
EE	HL	6.652	1,58	**0.012***			
Ear	HL	2.322	1,58	0.133	3.292	1,59	0.075
IN	HL	0.393	1,57	0.533	0.635	1,58	0.429

(ii)

y	**x**	**a**	**b**	**r**	**s.e.**	**n**	**C_{90}**	**C_{117}**
Males								
AGL	SVL	0.919	0.618	0.742	0.166	26	42.9	42.0
TW	SVL	0.852	0.175	0.575	0.248	25	9.0	8.6
FLL	SVL	1.013	0.149	0.894	0.101	26	15.8	15.9
HLL	SVL	1.149	0.093	0.916	0.101	26	18.2	18.9
HW	HL	0.590	3.050	0.691	0.124	26	79.6	72.5
SL	HL	0.659	1.254	0.850	0.082	26	41.0	37.9
EN	HL	0.590	1.191	0.732	0.110	26	31.1	28.3
EE	HL	0.661	0.969	0.693	0.138	26	31.9	29.5
Females								
AGL	SVL	1.182	0.189	0.989	0.030	35	42.9	45.0
TW	SVL	1.159	0.040	0.935	0.075	35	8.2	8.5
FLL	SVL	1.039	0.128	0.992	0.023	34	15.3	15.4
HLL	SVL	1.034	0.153	0.993	0.022	35	17.8	18.0
HW	HL	0.979	0.805	0.951	0.055	34	75.1	74.8
SL	HL	0.927	0.502	0.974	0.038	34	39.5	38.9
EN	HL	0.961	0.332	0.977	0.037	34	29.2	29.0
EE	HL	1.069	0.242	0.960	0.054	34	30.3	30.8

Allometry in the relationships between characters for the same lineage was tested by regression of the log-transformed character against ln(SVL) or ln(HL), and considered to exist if the slope of the regression line was more than two standard errors from 1.0 (Zar 1974). Sexes were analysed separately where sexual dimorphism was present, and pooled where sexual dimorphism was not present. Most characters showed significant allometry (Tables 4, 5). The effect of allometry was removed by converting the measurements to the values they would assume for an animal of average size, treating the sexes separately when sexual dimorphism was present, using the methods of Thorpe (1975). Mean values of SVL and HL (used as the independent variables for transforming other measurements) for the Cooktown lineage were very close to the overall means for the entire Australian *Cyrtodactylus* sample, and the range of variation for the Cooktown lineage extensively overlapped the overall range for Australian samples. As the other Australian lineages were represented by many fewer specimens and in some cases narrow size ranges, precluding assessments of sexual dimorphism and allometry for those lineages, we used the data for the Cooktown lineage alone to transform the values for all Australian samples.

For scalational characters and adjusted measurements, we first tested for the presence of differences between means of the genetic lineages by one-way analysis of variance, and only considered characters for the multivariate analyses that showed significant differences among the lineages. We chose to include in the multivariate analyses a set of four scalational characters (femoroprecloacal scales, transventral scales, longitudinal rows of dorsal tubercles, total lamellae below fourth toe), one untransformed measurement (SVL), and nine transformed measurements (adjusted AGL, TW, HLL, HW, HD, IN, EN, EE, EAR). This number of characters is sufficiently large to approximate the total pattern of variation (Thorpe 1989). Some additional characters that showed significant lineage differences were excluded because they showed low variation (e.g., labial scales) or showed similar patterns of variation to characters included (e.g., other toe lamellae counts, FLL (cf. HLL), SL (cf. EN)). We also were unable to include in the analyses some categorical features of scalation and coloration that distinguished genetic lineages. Two analyses were run, one for females, one for males. For the female analysis, all five lineages were treated as operational taxonomic units (OTUs), while for the male analysis only four lineages were treated as OTUs. The single male individual from the Tozer's Gap lineage was treated as of unknown identity.

RESULTS

Genetics

Australian taxa. The Bayesian consensus tree (Fig. 3) clearly shows that Australian *Cyrtodactylus* populations represent five completely supported lineages corresponding to geographically constrained clusters (Pascoe River, Tozer's Gap, McIlwraith Range, a broad group centred over Cooktown, and a southern group extending to Chillagoe) with posterior probabilities of 1.00 for all five groups. These five lineages formed two major clusters, one consisting of the Pascoe River and McIlwraith populations, the other of the Tozer's Gap, Cooktown and Chillagoe–Mungana Caves lineages. Average uncorrected sequence divergence within each of the five Australian lineages ranged from 0.00% (Pascoe River) up to 5.78% (Chillagoe–Mungana Caves) (Table 2). Among the Australian lineages, average uncorrected sequence divergence estimates ranged from 8.53% (Pascoe River *vs* McIlwraith) up to 17.72% (Tozer's Gap *vs* McIlwraith) (Table 2). There is marked population structuring within the Chillagoe lineage with two strongly supported subgroups, separating the Chillagoe–Mungana Caves individuals from the Parrot Creek Falls individuals located further north.

PNG and Solomon Island taxa. The Bayesian analysis shows that the three samples from the Solomon Islands form a monophyletic group with posterior probability of 1.00. Given that this lineage includes the *C. salomonensis* holotype from Ysabel Island (though only 650bp of this individual's ND2 gene was able to be sequenced), all three samples were therefore considered to belong to *C. salomonensis*.

The tree also shows that the *C. louisiadensis* group of previous authors (i.e., the Australian lineages together with *C. salomonensis* and the New Guinea species *C. epiroticus*, *C. klugei*, *C. lousiadensis*, *C. robustus* and *C. tripartitus*) is not monophyletic, as at least two species (*C. novaeguineae* and *C. zugi*; posterior probability 1.00) and possibly four (*C. sermowaiensis* and *C. loriae*; posterior probability 0.68) are nested between the Australian and non-Australian members of the putative *C. louisiadensis* group.

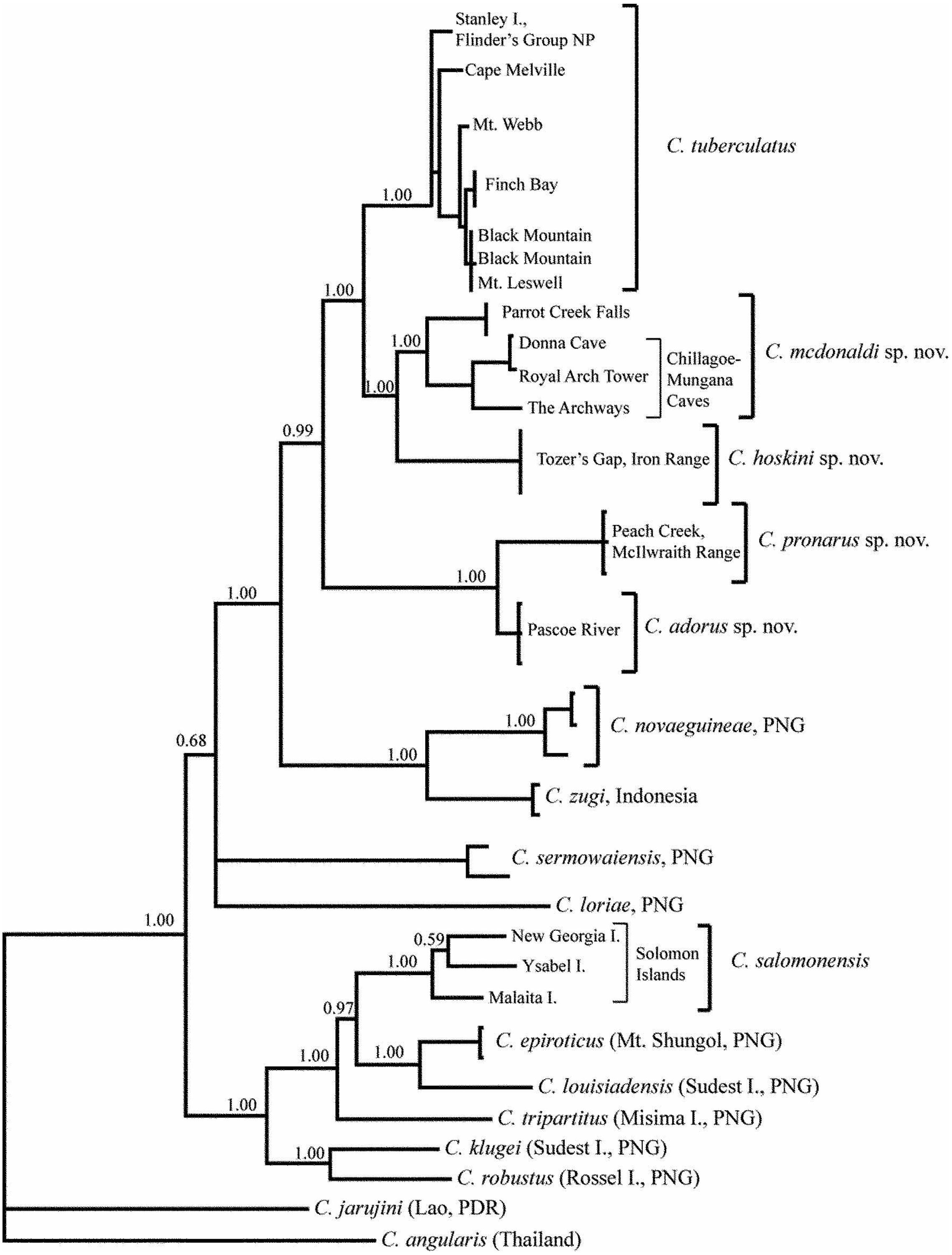

FIGURE 3. Bayesian consensus tree of *Cyrtodactylus* spp. based on mitochondrial ND2 sequences. Posterior probabilities are detailed above the branches. Branches with < 60% support were collapsed.

However, the New Guinea species of the *C. louisiadensis* group do form a strongly supported monophyletic group with *C. salomonensis* (posterior probabilities of 1.00 and bootstrap support 98%), exclusive of the other PNG species included in our analyses. The New Guinean species within the *C. louisiadensis* group differ on average from *C. salomonensis* by 15.02% as opposed to 19.90% from the other PNG species. Within the New Guinean *C. louisiadensis* group, average sequence divergence among the species ranges from 10.90% (between *C. epiroticus* and *C. louisiadensis*) up to 17.44% (between *C. louisiadensis* and *C. robustus*) (Table 3).

Interestingly, in the one instance in which two New Guinean species of the *C. louisiadensis* complex are known to occur sympatrically (*C. louisiadensis* and *C. klugei* on Sudest Island), the two species are not sister taxa. Such results are suggestive of multiple, independent colonisations of this island rather than *in situ* speciation from a common ancestor.

Finally, the tree clearly shows that the five Australian *Cyrtodactylus* lineages are not an extension of a geographic cline within an expanded *C. louisiadensis*.

Morphology

Testing the hypothesis of clinal variation within an expanded *Cyrtodactylus louisiadensis.* Within the Solomon Islands arc, the relationships of femoroprecloacal pores and enlarged femoroprecloacal scales against longitude were not significant (pores: $r^2 = 0.032$; $F_{1,15} = 0.500$, $P = 0.490$; scales: $r^2 = 0.061$; $F_{1,45} = 2.928$, $P = 0.094$). Number of transventral scales was significantly related to longitude ($r^2 = 0.405$; $F_{1,47} = 31.987$, $P < 0.001$) with a general decrease from north-west to south-east. However, the pattern of variation was not clinal, with the south-eastern-most individuals reverting to relatively high counts (a pattern also seen in pore and femoroprecloacal scale counts, in which the lowest counts were at intermediate localities).

Within the New Guinea arc, the relationship of femoroprecloacal pores to longitude was not significant ($r^2 = 0.056$; $F_{1,31} = 1.856$, $P = 0.183$), but significant relationships were present for femoroprecloacal scales ($r^2 = 0.259$; $F_{1,82} = 28.664$, $P < 0.001$) and transventral scales ($r^2 = 0.463$; $F_{1,82} = 70.835$, $P < 0.001$), with both increasing at the south-eastern end of the distribution, representing the Louisiade Archipelago. The pattern of variation was again not evenly clinal, with an apparent clinal decrease from north-west to south-east along the New Guinea coastline, and inter-island variation in the Louisiade Archipelago.

Within the Australian arc, all three characters showed a significant negative correlation with latitude, so that counts were lowest in the south-east (pores: $r^2 = 0.774$; $F_{1,53} = 154.349$, $P < 0.001$; femoroprecloacal scales: $r^2 = 0.517$; $F_{1,135} = 142.428$, $P < 0.001$; transventral scales: $r^2 = 0.245$; $F_{1,129} = 41.787$, $P < 0.001$). However, in each case (Fig. 4), the distribution was categorical rather than clinal, with high counts in the north and low counts in the south, and for femoroprecloacal scales, two groups were evident in the north, one with high counts, and the other with low counts. This reflects the two major genetic lineages of Australian species.

Variation among the Australian populations. There are consistent differences in colour pattern and scalation between the five genetic lineages, and between the two major clusters of lineages (see Comparisons with other species, in each species account). However, we were unable to find morphological differences between the two genetic subgroups in the Chillagoe lineage.

Multivariate analyses. Both female and male analyses provided high levels of discrimination of the Australian lineages.

Females (Fig. 5, Table 3). The first factor, which explained 75.6% of the total dispersion, provided complete separation between the two major lineages identified in the genetic analysis, the Pascoe River/McIlwraith group, and the Tozer's Gap, Cooktown and Chillagoe groups. The second factor, which explained 18.2% of the total dispersion, separated the two southern lineages within the second major lineage, with the geographically distant Tozer's Gap population being morphologically intermediate. The third factor, which explained 5.1% of the dispersion largely separated the Tozer's Gap population from the two southern lineages. The fourth factor, explaining 1.1% of the dispersion, provided separation of the Pascoe River from the McIlwraith group (scores -1.79 to +0.25 *vs* +0.45 to +1.92). Overall, the multivariate analysis correctly identified almost all individuals (98.5%, n = 67). The only misidentified individual was one from Pascoe River, which was identified as a McIlwraith animal, although it was still outside the range of McIlwraith individuals on Factor 4 scores.

Males (Fig. 6, Table 3). The first factor, which explained 86.3% of the total dispersion, again provided complete separation beween the two major lineages. The second factor, explaining 10.0% of the dispersion, distinguished the two southern lineages (Cooktown and Chillagoe), and partially separated the Pascoe River and McIlwraith lineages, while the third factor, explaining 3.7% of the dispersion, provided further separation of the latter two lineages. For all three factors, the single Tozer's Gap male (treated as unclassified) was closest to the Cooktown/Chillagoe lineages, but either intermediate between them, or slightly outside the values for either. Overall, the multivariate analysis correctly identified all individuals of the four OTUs (n = 49). The Tozer's Gap male was identified as closest to the Chillagoe lineage, although it is geographically most distant from it.

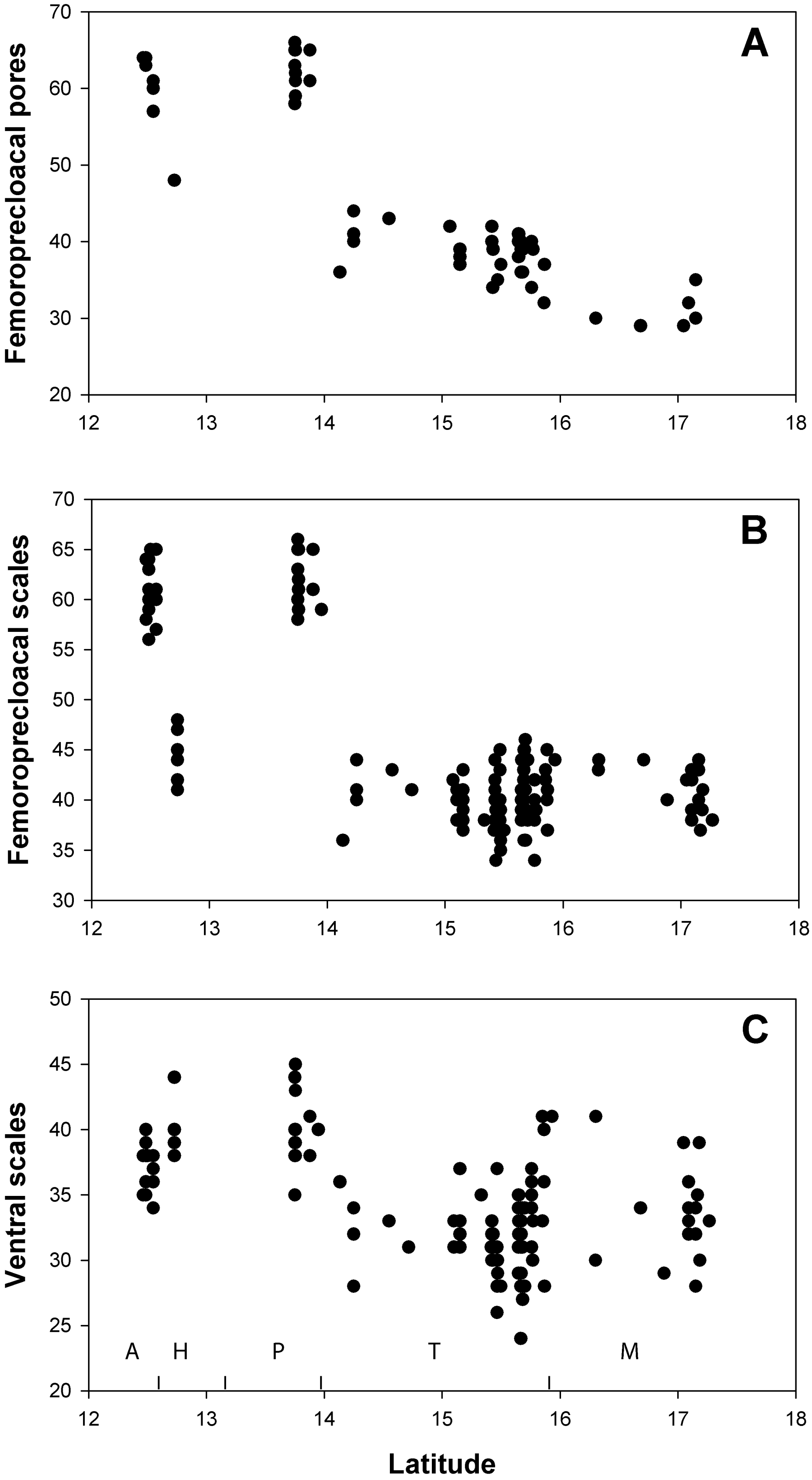

FIGURE 4. Latitudinal variation in (A) femoropreclocacal pores, (B) enlarged femoroprecloacal scales and (C) transventral scales among Australian *Cyrtodactylus*. Letters on lowest plot indicate species (first letter of specific epithet) defined later in the paper.

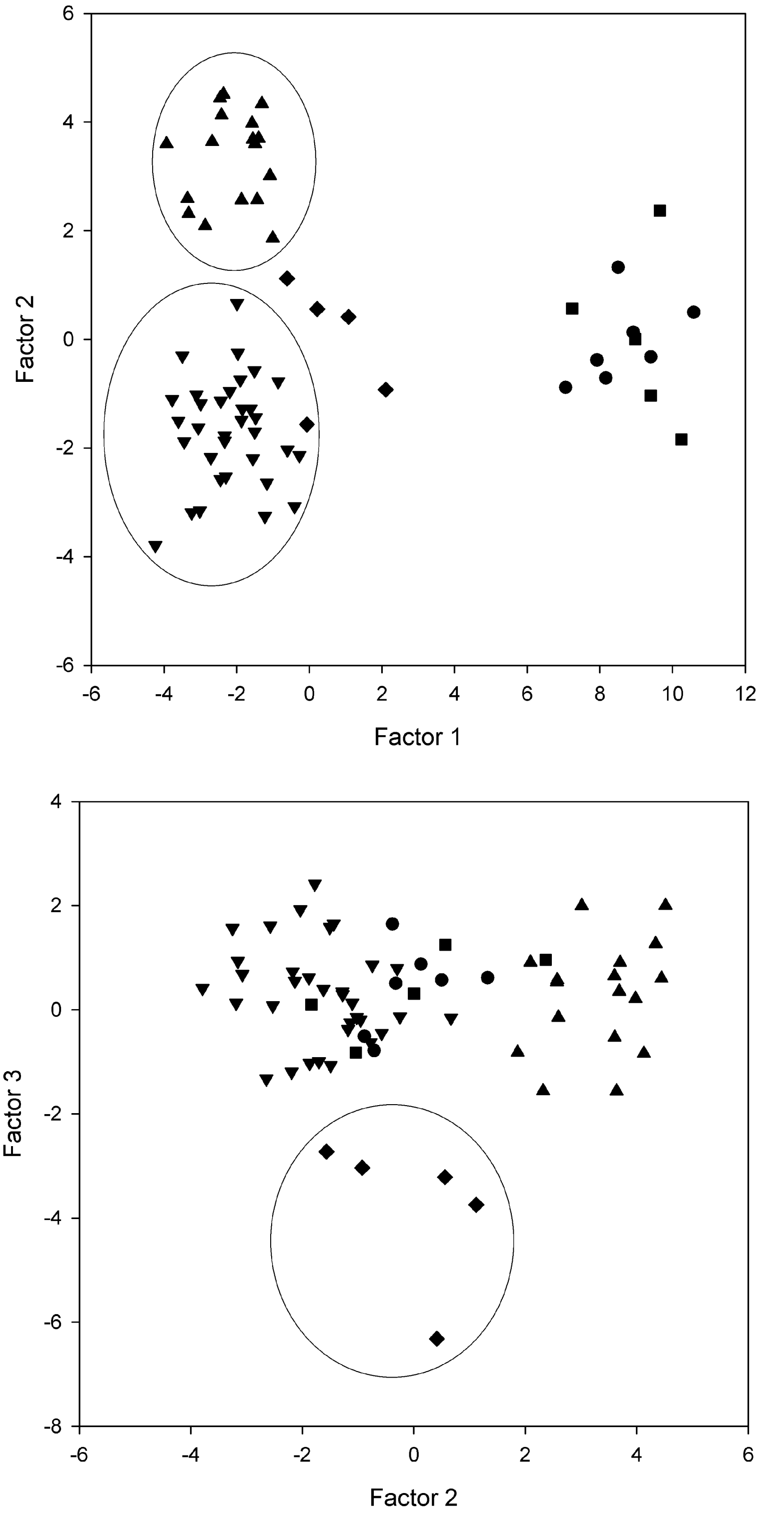

FIGURE 5. Scatterplots of scores from discriminant functions for female *Cyrtodactylus* from Australia. Inverted triangles = *C. tuberculatus* (Cooktown population), upright triangles *C. mcdonaldi* **sp. nov.** (Chillagoe population), diamonds = *C. hoskini* **sp. nov.** (Tozer's Gap population), circles = *C. adorus* **sp. nov.** (Pascoe River population), squares = *C. pronarus* **sp. nov.** (McIlwraith population). Ellipses highlight differentiation of *C. tuberculatus* and *C. mcdonaldi* from each other (Factor 2) and *C. hoskini* (Factor 3).

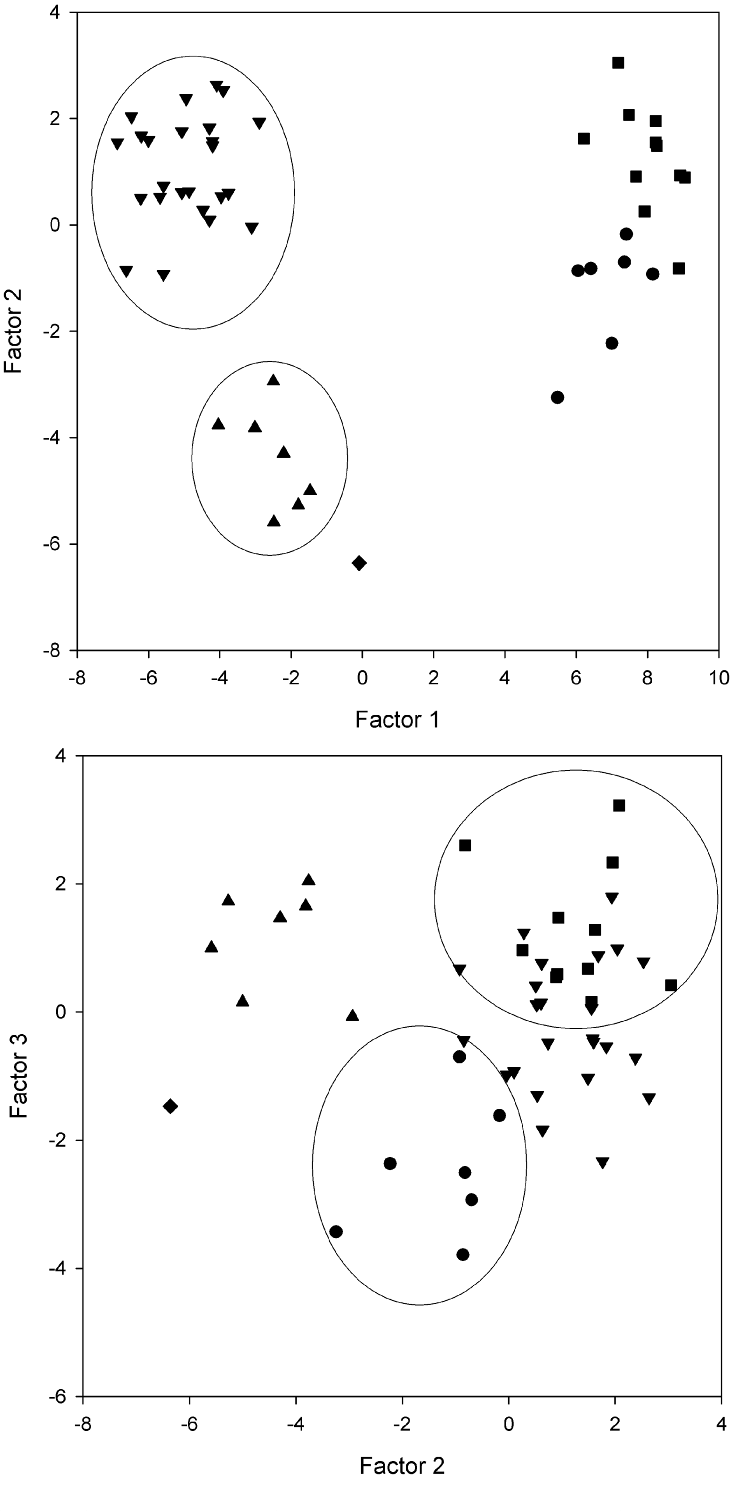

FIGURE 6. Scatterplots of scores from discriminant functions for male *Cyrtodactylus* from Australia. Inverted triangles = *C. tuberculatus* (Cooktown population), upright triangles *C. mcdonaldi* **sp. nov.** (Chillagoe population), diamond = *C. hoskini* **sp. nov.** (Tozer's Gap population), circles = *C. adorus* **sp. nov.** (Pascoe River population), squares = *C. pronarus* **sp. nov.** (McIlwraith population). Ellipses highlight differentiation of *C. tuberculatus* and *C. mcdonaldi* from each other (Factor 2) and *C. adorus* from *C. pronarus* (Factor 3).

DISCUSSION

Systematics of the Australian *Cyrtodactylus*. The inconsistent patterns of morphological variation among *Cyrtodactylus louisiadensis* sensu lato, together with the levels of genetic variation between the populations, are incompatible with the hypothesis of a single wide-ranging species, as previously argued by Kraus (2008) on morphological grounds alone for the New Guinea populations.

The five geographically discrete genetic lineages identified among the Australian populations are also distinguishable morphologically, with both data sets showing the same pattern of clustering of lineages. While there is not yet evidence of geographic overlap that would allow for assessment of species boundaries by direct application of the interbreeding criteria of the biological species concept, there are two instances where there is close geographic approach. The Chillagoe and Cooktown lineages approach to within 3 km, without evidence of either morphological intermediacy (Figs. 7, 8) or mixing of mitochondrial haplotypes, arguing for their recognition as separate species, although both belong to the same major lineage. In the far north, the Tozer's Gap and Pascoe River lineages, which belong to different major lineages, approach to within 20 km, again without any morphological intermediacy or haplotype mixing. As the degrees of genetic and morphological differentiation of the remaining combinations of lineages are within the spectrum represented by these two species pairs, we treat all five Australian lineages as discrete species.

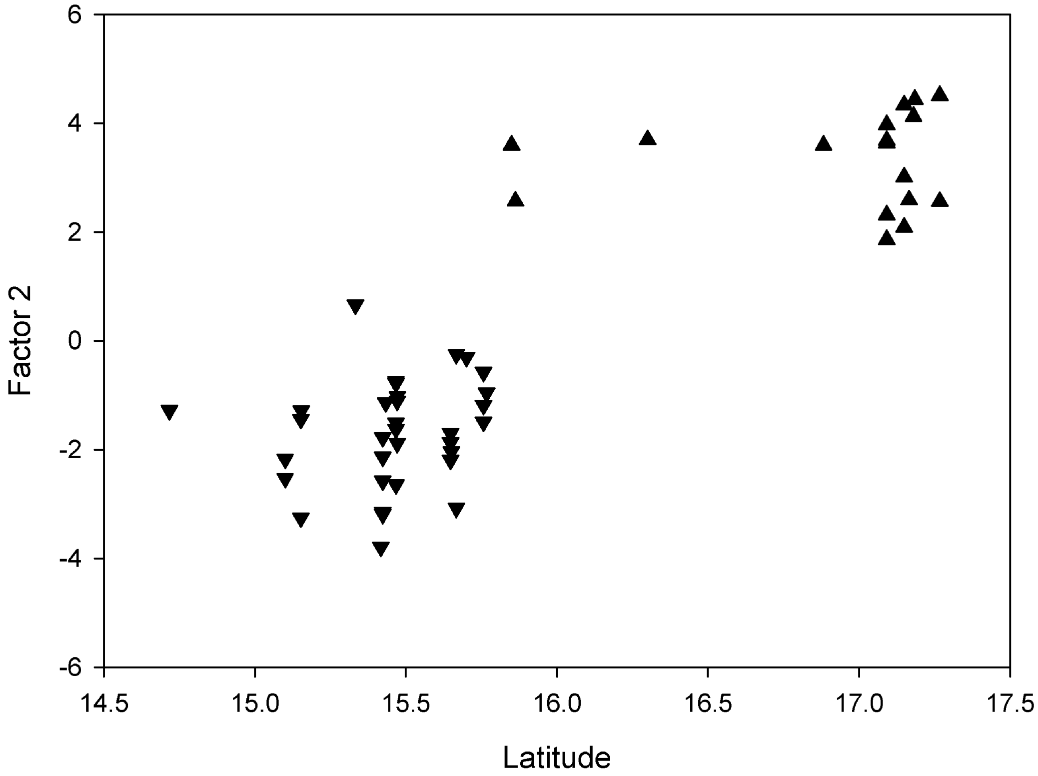

FIGURE 7. Latitudinal variation in function 2 scores for Cooktown and Chillagoe lineage females. Symbols as for Fig. 5.

The only two type specimens nominally from Australian localities are nested geographically within the Cooktown lineage, and morphologically accord with that lineage. Hence, the Cooktown lineage should be known as *Cyrtodactylus tuberculatus*. The remaining four lineages are treated as undescribed species, and named herein: *C. adorus* **sp. nov.** for the Pascoe River lineage, *C. pronarus* **sp. nov.** for the McIlwraith lineage, *C. hoskini* **sp. nov.** for the Tozer's Gap lineage, and *C. mcdonaldi* **sp. nov.** for the Chillagoe lineage.

While our phylogenetic analysis suggests that the Australian *Cyrtodactylus* species are a monophyletic group, our genetic comparisons are insufficiently extensive in their sampling across other regional *Cyrtodactylus* species to provide categorical certainty. However, they do provide strong evidence that the *Cyrtodactylus louisiadensis* group, as proposed by previous authors either as a single species (e.g., Brown & Parker 1973), or a complex of species (e.g., Brown & McCoy 1980; Kraus & Allison 2006; Kraus 2008; Rösler *et al*. 2007), is not monophyletic.

Hence, justification of the Australian taxa as distinct species needs to be based on morphological comparison with non-Australian taxa as well as within the Australian region. Given the large number of non-Australian species involved, we here provide a summary of characters that distinguish all the Australian species from most of the non-Australian species, and restrict our more detailed comparisons among species to those that are not excluded by this initial suite of character states.

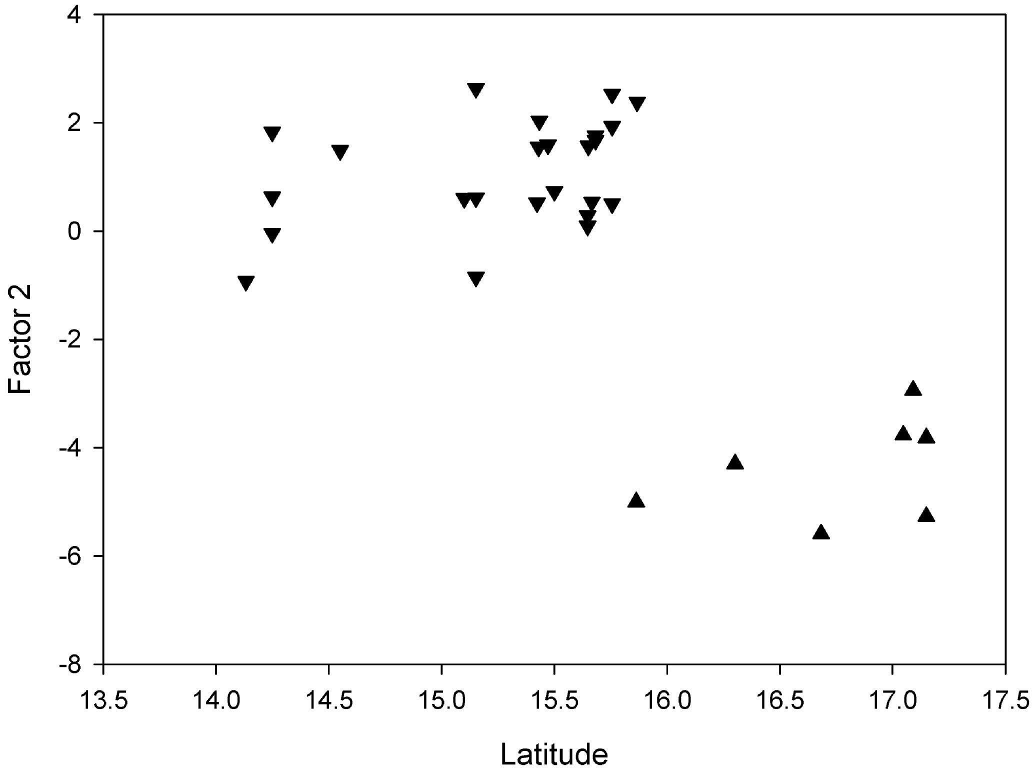

FIGURE 8. Latitudinal variation in function 2 scores for Cooktown and Chillagoe lineage males. Symbols as for Fig. 6.

All five Australian species have an extensive series of precloacal and femoral pores (totalling 29 or more) that reach the knee, and are distinguishable from taxa that lack femoral pores (*adleri* Das 1997, *angularis, annulatus* (Taylor 1915), *aurensis* Grismer 2005, *ayeyarwadyensis* Bauer 2003, *badenensis* Nguyen *et al*. 2006, *batik* Iskandar *et al*. 2011, *brevidactylus* Bauer 2002, *cattienensis* Geissler *et al*. 2009, *cavernicolus* Inger & King 1961, *chauquangensis* Hoang *et al*. 2007, *chrysopylos* Bauer 2003, *condorensis* (Smith 1921), *consobrinoides* (Annandale 1905), *cracens* Batuwita & Bahir 2005, *cryptus* Heidrich *et al*. 2007, *durio* Grismer *et al*. 2010, *edwardtaylori* Batuwita & Bahir 2005, *eisenmanae* Ngo 2008, *elok* Dring 1978; *fraenatus* (Günther 1864), *gansi* Bauer 2003, *gordongekkoi* (Das 1993), *grismeri* Ngo 2008, *hontreensis* Ngo *et al*. 2008, *ingeri* Hikida 1990, *irregularis* (Smith 1921), *jambangan* Welton *et al*. 2010a, *jarakensis* Grismer *et al*. 2008, *jarujini*, *jellesmae* (Boulenger 1897), *khasiensis* (Jerdon 1870), *laevigatus* (Darevsky 1964), *lateralis* (Werner 1900), *leegrismeri* Chan & Norhayati 2010, *malayanus* (de Rooij 1915), *malcolmsmithi* (Constable 1949), *mandalayensis* Mahony 2009, *martini* Ngo 2011, *matsuii* Hikida 1990, *nigriocularis* Nguyen *et al*. 2006, *nuaulu* Oliver *et al*. 2009, *oldhami* (Theobald 1876), *pageli* Schneider *et al*. 2011, *pantiensis* Grismer *et al*. 2008, *papilionoides* Ulber & Grossmann 1991, *papuensis*, *paradoxus* (Darevsky & Szczerbak 1997), *peguensis* (Boulenger 1893), *philippinicus* (Steindachner 1867), *phuquocensis* Ngo *et al*. 2010, *pseudoquadrivirgatus* Rösler *et al*. 2008, *pubisulcus* Inger 1958, *quadrivirgatus* Taylor 1962, *ramboda* Batuwita & Bahir 2005, *semenanjungensis* Grismer & Leong 2005, *sermowaiensis*, *soba* Batuwita & Bahir 2005, *spinosus* Linkem *et al*. 2008, *stresemanni* Rösler & Glaw 2008, *subsolanus* Batuwita & Bahir 2005, *sumonthai* Bauer *et al*. 2002, *sworderi* (Smith 1925), *tautbatorum* Welton *et al*. 2009, *thirakhupti* (Pauwels *et al*. 2004), *wakeorum* Bauer 2003, *wallacei* Hayden *et al*. 2008, *wayakonei* Nguyen *et al*. 2010, *yangbayensis* Ngo & Chan 2010, *yoshii* Hikida 1990 and *zhaoermii* Shi & Zhao 2010), and those that have 12 or fewer femoral pores, or a total femoroprecloacal pore count of 26 or fewer (*aequalis* Bauer 2003, *agusanensis* (Taylor 1915), *auribalteatus* Sumontha *et al*. 2010, *baluensis* (Mocquard 1890), *bichnganae* Ngo & Grismer 2010, *brevipalmatus* (Smith 1923), *caovansungi* Orlov *et al*. 2007, *consobrinus* (Peters 1871), *dumnuii* Bauer *et al*. 2010, *gubaot* Welton *et al*. 2010b, *gubernatoris* (Annandale 1913), *huynhi* Ngo & Bauer 2008, *interdigitalis* Ulber 1993, *intermedius* (Smith 1917), *mamanwa* Welton *et al*. 2010b, *marmoratus* Gray 1831, *redimiculus* King 1962, *sumuroi* Welton *et al*. 2010b, *takouensis* Ngo & Bauer 2008, *tigroides* Bauer *et al*. 2003 and *ziegleri* Nazarov *et al*. 2008.

The Australian species, all of which attain snout-vent lengths of 100 mm or more, are distinguishable from the following species, which have maximum recorded adult lengths of 80 mm or less: *adleri*, *agamensis* (Bleeker 1860), *annandalei* Bauer 2003, *annulatus*, *ayeyarwadyensis*, *badenensis*, *batucolus* Grismer *et al*. 2008, *brevipalmatus*, *capreoloides* Rösler *et al*. 2007, *cattienensis*, *chanhomeae* Bauer *et al*. 2003, *chrysopylos*, *consobrinoides*, *durio*, *elok*, *erythrops* Bauer *et al*. 2009, *feae* (Boulenger 1893), *fumosus* (Müller 1895), *gansi*, *gordongekkoi*, *gubernatoris*, *huynhi*, *ingeri*, *interdigitalis*, *irregularis*, *jambangan*, *jarakensis*, *jellesmae*, *laevigatus*, *lomyenensis* Ngo & Pauwels 2010, *marmoratus*, *oldhami*, *pantiensis*, *papuensis*, *pubisulcus*, *quadrivirgatus*, *redimiculus*, *roesleri* Ziegler *et al*. 2010, *rubidus* (Blyth 1860), *semenanjungensis*, *seribuatensis* Youmans & Grismer 2006, *sumonthai*, *sworderi*, *tautbatorum*, *thirakhupti*, *variegatus* (Blyth 1859), *wakeorum*, *wetariensis* (Dunn 1927) and *zhaoermii*.

The Australian species are all strongly banded, and hence are distinguishable from the following species that have irregular, blotched or striped dark patterning, or have broken bands: *adleri*, *aequalis*, *agamensis*, *angularis*, *ayeyarwadyensis*, *baluensis*, *batucolus*, *biordinis*, *brevipalmatus*, *buchardi* David *et al*. 2004, *chauquangensis*, *condorensis*, *cryptus*, *darmandvillei* (Weber 1890), *elok*, *erythrops*, *fumosus*, *gordongekkoi*, *gubernatoris*, *ingeri*, *interdigitalis*, *irregularis*, *jarakensis*, *jarujini*, *khasiensis*, *laevigatus*, *lateralis*, *loriae*, *malayanus*, *malcolmsmithi*, *mandalayensis*, *marmoratus*, *martini*, *matsuii*, *nigriocularis*, *oldhami*, *pantiensis*, *papilionoides*, *papuensis*, *paradoxus*, *peguensis*, *pseudoquadrivirgatus*, *pubisulcus*, *quadrivirgatus*, *russelli* Bauer 2003, *sadleiri* Wells & Wellington 1985, *salomonensis* Rösler *et al*. 2007, *semenanjungensis*, *seribuatensis*, *sermowaiensis*, *serratus* Kraus 2007, *slowinskii* Bauer 2002, *spinosus*, *stresemanni*, *sworderi*, *tamaiensis* (Smith 1940), *teyniei* David *et al*. 2011, *variegatus*, *wetariensis*, *yoshii*, *zhaoermii* and *ziegleri*.

Among the remaining *Cyrtodactylus* species with banded coloration, the Australian species have wide pale and dark bands, and the dark bands consist of a nuchal band, a band over the shoulders, and modally three bands over the trunk, and hence differ from species having very narrow pale bands (*aaroni*, *aurensis*, *badenensis*, *batik*, *derongo* Brown & Parker 1973, *eisenmanae*, *grismeri*, *mimikanus*, *redimiculus*, *wallacei* and *wayakonei*), those having very narrow dark bands on an overall pale background (*capreoloides*, *consobrinoides*, *gansi* and *wakeorum*), those having an extra dark band between the nuchal band and the shoulder band (*annandalei*, *bichnganae*, *chrysopylos* and *wakeorum*), one species which lacks a dark shoulder band (*badenensis*), species having only two dark bands across the trunk (*batik*, *caovansungi*, *deveti* Brongersma 1948, *hontreensis*, *irianjayaensis* Rösler 2001, *murua*, *phongnhakebangensis* Ziegler *et al*. 2002, *sumonthai*, *tiomanensis* Das & Lim 2000 and *zugi* Oliver *et al*. 2008), and those having modally five dark bands across the trunk (*aaroni*, *boreoclivus* Oliver *et al*. 2011, *chrysopylos*, *consobrinoides* and *halmahericus* (Mertens 1929)).

The Australian species have a single row of transversely oriented broad median subcaudal scales, and hence differ from the following species, which have small subcaudal scales: *adleri*, *agamensis*, *agusanensis*, *annulatus*, *ayeyarwadyensis*, *batucolus*, *biordinis*, *brevidactylus*, *brevipalmatus*, *buchardi*, *capreoloides*, *cattienensis*, *cavernicolus*, *cryptus*, *deveti*, *durio*, *elok*, *fumosus*, *gansi*, *gordongekkoi*, *gubaot*, *gubernatoris*, *huynhi*, *interdigitalis*, *irianjayaensis*, *irregularis*, *jambangan*, *jarakensis*, *jellesmae*, *lateralis*, *loriae*, *mamanwa*, *mandalayensis*, *marmoratus*, *martini*, *matsuii*, *novaeguineae*, *nuaaulu*, *pantiensis*, *papilionoides*, *papuensis*, *philippinicus*, *pubisulcus*, *quadrivirgatus*, *sadleiri*, *semenanjungensis*, *seribuatensis*, *sermowaiensis*, *serratus*, *spinosus*, *stresemanni*, *sumuroi*, *sworderi*, *tamaiensis*, *tautbatorum*, *tigroides*, *tiomanensis*, *wakeorum*, *wallacei*, *wetariensis*, *yoshii*, *zhaoermii*, *ziegleri* and *zugi*.

Like most *Cyrtodactylus* species, the Australian species lack a precloacal groove, and hence differ from the following species, which have either a longitudinal or transverse precloacal groove: *agamensis*, *annulatus*, *aurensis*, *cavernicolus*, *fumosus*, *gansi*, *halmahericus*, *jambangan*, *macrotuberculatus* Grismer & Norhayati 2008, *marmoratus*, *nuaaulu*, *papuensis*, *philippinicus*, *pubisulcus*, *pulchellus* Gray 1827, *rubidus*, *semenanjungensis*, *spinosus*, *stresemanni* and *tautbatorum*.

The Australian species have between 24-45 longitudinal rows of ventral scales between the ventrolateral skin folds at midbody, and differ from the following species, which have either fewer than 24 rows (*aequalis*, *macrotuberculatus* and *variegatus*), or 45 or more rows (*adleri*, *agamensis*, *agusanensis*, *annulatus*, *aurensis*, *batik*, *brevi-*

dactylus, *cavernicolus*, *consobrinoides*, *cryptus*, *derongo*, *durio*, *gubaot*, *halmahericus*, *jambangan*, *jarakensis*, *lateralis*, *malayanus*, *mamanwa*, *matsuii*, *papuensis*, *philippinicus*, *semenanjungensis*, *stresemanni*, *sumoroi*, *tautbatorum*, *wallacei*, *yoshii* and *zugi*).

Finally, the Australian species usually have between 20–24 longitudinal rows of dorsal tubercles on the body (occasionally as low as 18 or as high as 25), and differ from the following species, which have fewer than 20 tubercle rows (*adleri*, *agamensis*, *annandalei*, *annulatus*, *aurensis*, *batucolus*, *bichnganae*, *biordinis*, *boreoclivus*, *brevipalmatus*, *caovansungi*, *chanhomeae*, *chauquangensis*, *chrysopylos*, *cracens*, *darmandvillei*, *durio*, *edwardtaylori*, *eisenmanae*, *elok*, *fraenatus*, *fumosus*, *halmahericus*, *hontreensis*, *huynhi*, *ingeri*, *intermedius*, *jambangan*, *jarakensis*, *lateralis*, *leegrismeri*, *malcolmsmithi*, *mandalayensis*, *marmoratus*, *martini*, *matsuii*, *migriocularis*, *nuaaulu*, *pageli*, *papilionoides*, *paradoxus*, *philippinicus*, *phongnhakebangensis*, *ramboda*, *redimiculus*, *roesleri*, *serratus*, *soba*, *spinosus*, *stresemanni*, *subsolanus*, *sumonthai*, *takouensis*, *tautbatorum*, *teyniei*, *thirakhupti*, *tigroides*, *wayakonei*, *wetariensis* and *yoshii*), or 25 or more tubercle rows (*brevidactylus*, *buchardi*, *epiroticus*, *louisiadensis*, *mamanwa*, *salomonensis*, *seribuatensis* and *tripartitus*) or have the tubercles scattered and not longitudinally aligned (*gordongekkoi* and *khasiensis*).

Hence, this combination of seven characters distinguishes the Australian species from all *Cyrtodactylus* other than *C. klugei* and *C. robustus.*

Conservation assessment. The change of status of Australian *Cyrtodactylus* from a single taxon conspecific with a widespread New Guinean and Solomon Islands species, to five endemic Australian taxa with non-overlapping distributions, has profound implications for the conservation status to be applied to each of these taxa. We here apply IUCN criteria (IUCN Standards and Petitions Subcommittee 2010) to the Australian taxa.

Systematics

Cyrtodactylus tuberculatus (Lucas & Frost 1900)

(Fig. 9)

Synonymy

Hoplodactylus tuberculatus Lucas & Frost 1900: 145. Holotype: MV D7874, Endeavour River (presented C. Frost, 2.x.1899)
Gymnodactylus olivii Garman 1901: 1. Holotype: MCZ 6470, near Cooktown (E.A.C. Olive, received by MCZ in 1896).

Diagnosis. A large *Cyrtodactylus* (SVL to 120 mm) with large, strongly projecting tubercles on the antebrachium, strongly developed dorsal tubercles in 20–24 longitudinal rows at the midpoint of the trunk (axilla-groin interval), 24–37 ventral scale rows at the same level, a continuous series of 34–46 enlarged femoroprecloacal scales extending from one knee to the other, and in males bearing pores on each scale; mental with a posterior extension extending between postmentals; lips marbled, dark dorsal bands on trunk usually three, occasionally four, with a narrow dark edge both anteriorly and posteriorly; pale interspaces between dark body bands with dark macules; dark tail bands on base of tail only a little wider than pale interspaces.

Description. Size large (males 78–116.5 mm, mean = 105.7 mm, sd = 7.74, n = 29; females 46–120 mm, mean = 95.1 mm, sd = 22.66, n = 42; combined 46–120 mm, mean = 99.4 mm, sd = 18.76, n = 71).

Head relatively long (HL/SVL 25.3–33.2%, mean = 29.1%; sd = 1.69, n = 62) and wide (HW/HL 66.5–88.0%, mean = 75.3%; sd = 5.67, n = 62, only two individuals greater than 77.8%), slightly depressed (HD/HL 35.3–57.5%, mean = 42.3%, sd = 4.56, n = 62), distinct from neck. Loreal region moderately inflated, canthus rostralis poorly defined. Interorbital region and top of snout concave, deepest and widest just anterior to level of rostral canthus of eye. Snout moderately long (SL/HL 36.3–45.1%, mean = 39.3%, sd = 2.12, n = 62; EN/HL 26.0–34.5%, mean = 29.3%, sd = 1.72, n = 62), much longer than eye diameter (SL/EYE 143.6–215.0%, mean = 173.7%, sd = 13.45, n = 63), and a little longer than eye-ear interval (EE/HL 25.8–36.9%, mean = 30.5%, sd = 2.31, n = 62). Eye large (EYE/HL 18.9–28.0%, mean = 22.7%, sd = 1.83, n = 62), pupil vertical with crenated margin, forming about 3-4 low lobes along each edge of pupil. Supraciliaries in a double row, large, frill-like, well-differentiated from adjacent, more medial granules of the brow ridge, and largest anteriorly. Ear opening small (EAR/HL 7.1–12.3%, mean = 9.7%, sd = 1.21, n = 62), usually a little taller than long and slightly angled posterodorsally, but sometimes rounder. Rostral wider than high, height at centre less than that more laterally, divided dorsally by a median groove that extends about ⅓–½ the midline height of the scale, and fails to reach the oral margin. Two enlarged supranasals separated by usually a single, less enlarged internasal. External nares circular, bordered by first supralabial, rostral, supranasal, nasal (extending into posterior part of nostril) and 3-4 smaller granular scales between nasal and first supralabial. Nares moderately separated (IN/HL 11.3–17.2%, mean = 13.5%, sd = 1.23, n = 61). Supralabials anteriorly large, distinct from adjacent loreal granules, 8–11 (mode = 9 (53.2%), mean = 8.8, sd = 0.77, n = 62) to level of mid-orbit, then inflecting dorsally and posteriorly, and becoming smaller, to gradually blend along rictal margin with adjacent small granules; supralabials separated from orbital margin by at least two rows of small granular scales at narrowest point. Mental wider than deep, with a strong median extension, a little to moderately narrower than rostral, and bordered posteriorly by a single elongate pair of large postmentals (Fig. 10A). Infralabials anteriorly much larger than adjacent gular scales, becoming smaller posteriorly, 8–12 (mode = 10 (44.4%), mean = 10.0, sd = 0.87, n = 63). First infralabial with ventral border formed approximately ⅔ by postmental, ⅓ by anteriormost enlarged subinfralabial. Subinfralabial scales anteriorly large, flattened, and polygonal, becoming smaller, more rounded and granular posteriorly and medially (towards gular area).

FIGURE 9. Living *Cyrtodactylus tuberculatus* from Black Mountain, Qld. (Photo: P. Couper).

Body moderately robust (AGL/SVL 36.7–49.7%, mean = 43.0%, sd = 2.93, n = 63), with low, but distinct, ventrolateral skin folds approximately marking the transition between the enlarged flattened ventral scalation and the smaller, more rounded, granular lateral scalation. Scales on dorsum of head, body and limbs small, juxtaposed, rounded granules, with interspersed much larger tubercles. Granular scales finest over parietal region of head, becoming coarser over body, then more polygonal and flatter on tail. On head dorsum (Fig. 11A), tubercles small and only slightly projecting, anteriorly commencing in the posterior interocular area, becoming larger, more projecting and with a more conical, slightly posteriorly-tilted apex over nape. Tubercles on body dorsum larger again (Fig. 12A), but with a more longitudinally ovoid base, often with a weak median keel, and relatively low on anterior body, but becoming much more projecting posteriorly on body, over sacrum and onto tail base, where they are markedly conical. Tubercles persist along tail, two whorls per segment, becoming lower and less differentiated until eventually losing their distinction by about the fifth dark band. Large tubercles on body dorsum separated by 2–3 smaller granular scales, those on head and nape more widely separated by several scales. Tubercles on body arranged in about 20–25 (mean = 22.6, sd = 1.30, n = 63) roughly longitudinal rows. Dorsum of brachium with juxtaposed small scales and densely packed larger tubercles; antebrachium with more imbricate larger scales distally and over manus, and densely packed larger tubercles (Fig. 13A). Dorsum of thigh like brachium; of crus with small juxtaposed granules and densely packed large tubercles (Fig. 13F), only dorsum of pes with imbricate scales.

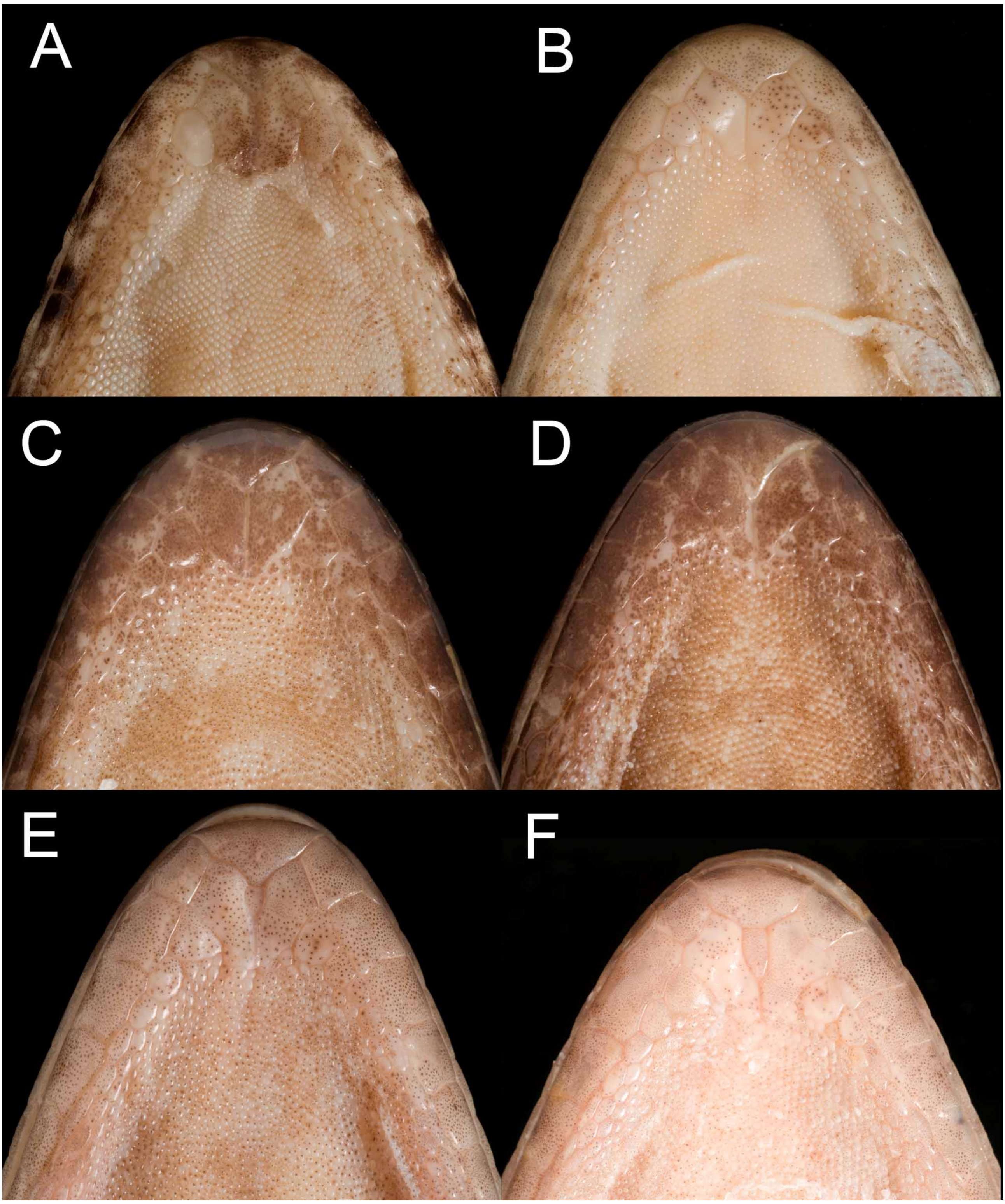

FIGURE 10. Chin shields of Australian *Cyrtodactylus* species. A. *C. tuberculatus* (QM J87009), B. *C. mcdonaldi* (QM J87075), C. *C. hoskini* (QM J86950), D. *C. adorus* (QM J86979), E. *C. pronarus* (QM J86900), F. *C. pronarus* (QM J86909).

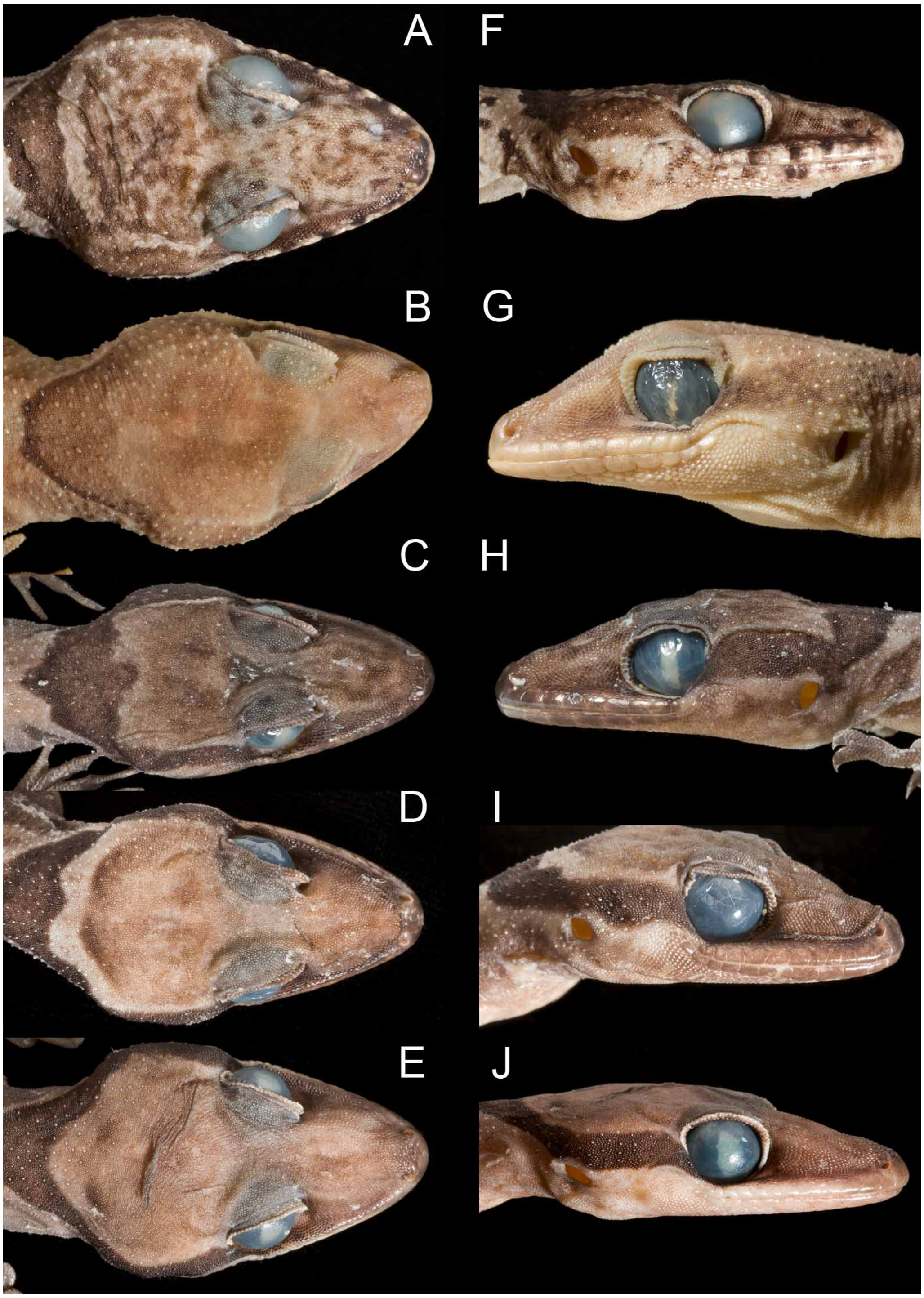

FIGURE 11. Dorsal (A-E) and lateral (F-J) aspects of head of Australian *Cyrtodactylus* species. A,F. *C. tuberculatus* (QM J87009), B,G. *C. mcdonaldi* (QM J30062), C,H. *C. hoskini* (QM J86950), D, I. *C. adorus* (QM J86979), E,J. *C. pronarus* (QM J86900).

Laterally, tubercles commence over temporal region and in postinfralabial area, where they are noticeably larger (Fig. 11F) than those of the head dorsum, then along nape and body, where they are smaller and noticeably less protuberant than those dorsally, and along tail, commencing on tail base as prominent, protuberant, conical scales, then rapidly losing differentiation by second dark tail band (Fig. 14A).

FIGURE 12. Dorsal aspect of trunk of Australian *Cyrtodactylus* species. A. *C. tuberculatus* (QM J87189), B. *C. mcdonaldi* (QM J87075), C. *C. hoskini* (QM J86950), D. *C. adorus* (QM J86979), E. *C. pronarus* (QM J86909).

FIGURE 13. Tubercles on front (A-E) and hind (F-J) limbs of Australian *Cyrtodactylus* species. A,F. *C. tuberculatus* (QM J87189), B,G. *C. mcdonaldi* (QM J87075), C,H. *C. hoskini* (QM J86950), D,I. *C. adorus* (QM J86979), E,J. *C. pronarus* (QM J86900).

FIGURE 14. Tubercles and colour pattern on tail base dorsum of Australian *Cyrtodactylus* species. A. *C. tuberculatus* (QM J87189), B. *C. mcdonaldi* (QM J30062), C. *C. hoskini* (QM J86950), D. *C. adorus* (QM J86979), E. *C. pronarus* (QM J86900).

Ventrally, gular scales small, rounded and juxtaposed, becoming larger, flat and more imbricate over body venter, from clavicular region. Ventral scales at midbody, between ventrolateral skin folds 24–37 (mean = 31.3, sd = 2.84, n = 68). Ventral scales on brachium and antebrachium like gular scales. On ventral surface of thighs, but not on crus or in precloacal region, an abrupt junction between enlarged imbricate scales and much smaller scales posteriorly, enlarged scales 34–46 between distal extent on each thigh (mean = 39.8, sd = 2.69, n = 71). Ventral scales of tail base like those of body, most of tail venter with a single median series of very broad scales about quadruple the width of adjacent ventrolateral scales.

Precloacal and femoral pores present in males, in a single continuous row, arching shallowly anteriorly in precloacal region. Pores 34–44 (mean = 38.9, sd = 2.57, n = 29), best developed in precloacal region where they are deep and transversely oriented, becoming much shallower, smaller and rounder distally under thigh. No pubic groove. About three large, blunt-tipped postcloacal spurs on ventrolateral surface of tail base, more projecting in adult males than females or juveniles.

Forelimbs and hindlimbs well-developed (FLL/SVL 13.2–17.0%, mean = 15.5%, sd = 0.72, n = 62; HLL/SVL 16.6–20.1%, mean = 18.2%, sd = 0.82, n = 63). Digits well-developed, reflected dorsally at proximal interphalangeal joint, and all bearing robust, strongly curved claws sheathed at the base by two scales. Subdigital lamellae expanded basally, beginning on pes over distal part of metatarsals and ending at point of reflection of toes, lamellae distal to this point not expanded. Lamellae under first toe 6–11 expanded (mean = 8.1, sd = 1.04, mode 8 (38.7%)) + 8–12 narrow (mean = 10.3, sd = 0.95, mode 10 (38.7%)), total 15–22 (mean = 18.5, sd = 1.49, mode 18 (33.9%), n = 62). Lamellae under second toe 8–11 expanded (mean = 9.6, sd = 0.71, mode 10 (50.8%)) + 10–13 narrow (mean = 11.4, sd = 0.87, mode 11 (42.9%)), total 19–24 (mean = 21.0, sd = 1.05, mode 21 (36.5%), n = 63). Lamellae under third toe 9–13 expanded (mean = 10.9, sd = 0.79, mode 11 (62.9%)) + 10–15 narrow (mean = 12.5, sd = 1.18, mode 13 (32.3%)), total 20–27 (mean = 23.4, sd = 1.46, mode 24 (29.0%), n = 62). Lamellae under fourth toe 10–16 expanded (mean = 13.2, sd = 1.28, mode 14 (31.7%)) + 11–16 narrow (mean = 12.9, sd = 1.09, mode 13 (36.5%)), total 22–30 (mean = 26.2, sd = 1.79, mode 26 (27.0%), n = 63). Lamellae under fifth toe 7–11 expanded (mean = 9.3, sd = 0.96, mode 9 (40.3%)) + 10–16 narrow (mean = 13.1, sd = 1.33, mode 14 (35.5%)), total 18–26 (mean = 22.4, sd = 1.72, n = 62). Relative lengths of digits on manus I<II<V<III<IV; on pes I<II<III=V<IV. Very slight traces of webbing between bases of fingers; weak webbing between bases of toes 2–3, 3–4 and 4–5.

Tail a little longer than body (TL/SVL 120.4–146.5%, mean = 127.9%, sd = 7.73, n = 11), narrow at base (TW/SVL 5.7–10.6%, mean = 8.4%, sd = 1.07, n = 62) and tapering evenly to a conical tip. Tail segments externally identifiable by straight scale junctions, segments about 5–7 scales long when counted to include tubercles. Cloacal sacs present in both sexes, larger in males, external orifices just posterior to vent, laterally.

Colour in preservative. Dorsal pale ground colour fawn. Head dorsum (Fig. 11A) coarsely mottled with mid to dark brown, bordered posterolaterally by a narrow pale band which may itself have a sharply delimited dark brown anterior edge. Pale nape zone bordered posteriorly by a U-shaped dark chevron on nape, widest vertebrally, and extending anteriorly over temporal region to eye, then usually weakly present over posterior lores. Second broad dark transverse dorsal band over shoulders, lateral margins extending more narrowly anteroventrally in front of forelimbs. Usually three (78.6%, n = 56), sometimes four (17.9%), rarely five (3.6%) dark bands over trunk, extending lateroventrally with even width, but dissipating over flanks. A dark band over hips. Tail with dark bands over most of length, but distal third of tail usually pale cream to white, with bands barely evident. When they can be counted to the distal end of tail, dark tail bands 11–16 (mean = 13.5, sd = 1.83, n = 12). On nape and body, dark bands of nearly equal width to pale interspaces, and with abrupt straight edges; pigmentation generally darkest along band margins, leaving centre of bands a little lighter. Bands on tail (Fig. 14A) of similar width to body bands, and equally spaced to pale interspaces, but darker and more solidly dark than those of body. Pale interspaces of body often with a few dark brown spots.

Upper and lower lips (Fig. 11F) mottled with mid-brown, mottling extending to postinfralabial area. Dorsum of forelimbs and hindlimbs similarly mid-brown mottled.

Entire ventral surface immaculate, cream to pale yellow.

Allometry. With respect to snout-vent length, AGL, TW, FLL and HLL are in positive allometry, while HL is in negative allometry; with respect to head length, HD, EYE, SL and IN are in negative allometry, while HW, EN, EE and EAR are in isometry (Table 4). Hence, small individuals will have proportionally shorter bodies and limbs, narrower tails and longer and deeper heads, larger eyes, and longer and wider snouts than large individuals (Table 5(i)).

Sexual dimorphism. Adult females have proportionally longer bodies (greater AGL/SVL) but narrower tails and shorter limbs than adult males of the same size (Table 5(ii)). While there are statistically significant differences in the shape of the head in some measurements, they are not consistent at all sizes, with adult males having wider heads (HW/HL), but longer snouts (SL/HL, EN/HL) and shorter postocular regions (EE/HL) than similarly sized females at the onset of maturity, but the differences being reversed at larger sizes. The range of variation in these head proportions extensively overlaps at all sizes, and the regression coefficients for the male values are generally lower than for the female data, which may be due to a paucity of small males resulting in a narrowing of the range of the independent variable, leading to less accuracy in the slope of the relationship. Consequently, these statistical differences may be artefactual.

Description of holotypes. The holotype of *Hoplodactylus tuberculatus* is an immature-sized female with SVL 82 mm, AGL 34 mm, TL 107 mm, TW 8.7 mm, HL 23.4 mm, HW 20.5 mm, HD 11.2 mm, IN 3.5 mm, SL 10.5 mm, EN 7.6 mm, EYE 5.7 mm, EE 8.0 mm, EAR 2.7 mm, FLL 12.7 mm, HLL 15.2 mm, lamellae below digits I-V 7+10, 10+12, 11+13, 12+12, 10+12 respectively, supralabials 10, infralabials 10, dorsal tubercle rows 24, transventral rows 31, enlarged femoroprecloacal scales 38, dark trunk bands 3, and dark tail bands *ca*. 11 (bands losing distinction towards tip). The specimen is poorly preserved posteriorly, with some loss of the body wall along the posterior trunk and disarticulated vertebrae. Some of the skin of the head crown and throat has been torn across and bunched, possibly as a result of damage at the time of collection. Kluge (1963) described the specimen as "moderately well preserved", although this may have been in comparison to the very poorly preserved, desiccated and disarticulated holotypes of other gecko species reported in the same paper. While Lucas and Frost (1900) report the SVL as 88 mm, this measurement is only attainable if the specimen is abnormally stretched. The decomposition of the posterior body cavity and concurrent loosening of the vertebrae in the region allow for this.

The holotype of *Gymnodactylus olivii* is an adult-sized female with SVL 105 mm, transventral scales 28, femoroprecloacal scales 39, and dark trunk bands three. The specimen is well preserved.

Although both holotypes are female and hence pores are not present, the femoropreanal scale count and coloration of both specimens is only compatible with the Cooktown species or with *C. mcdonaldi* n. sp. The holotype of *H. tuberculatus* lies close to the centre of the variation in Factor 2 scores for the Cooktown species (Fig. 5; score -1.62), and agrees in all coloration respects with the species. While we did not obtain a full set of counts and measurements from the holotype of *G. olivii*, it also agrees closely with the Cooktown species, particularly in the degree of tubercle development and the number of enlarged femoroprecloacal pores, which is much less than the range for any of the Papuan/Solomon Islands species (all of which have 59 or more enlarged scales), and we see no reason to doubt the type locality, which is close to the centre of the distribution of the species. Hence, we reject the hypothesis of Waite (1905) that the holotype of *G. olivii* is not from Australia.

Etymology. Not specifically stated by Lucas and Frost (1900), but presumably from the Latin *tuberculatus* (= tuberculate), and in allusion to the strongly developed dorsal tubercles of the species.

Distribution. Found on mainland Australia, from Cape Melville, south to Mt Leswell (Fig. 15). Also present on Stanley Island, in the Flinders Islands, just north of Cape Melville.

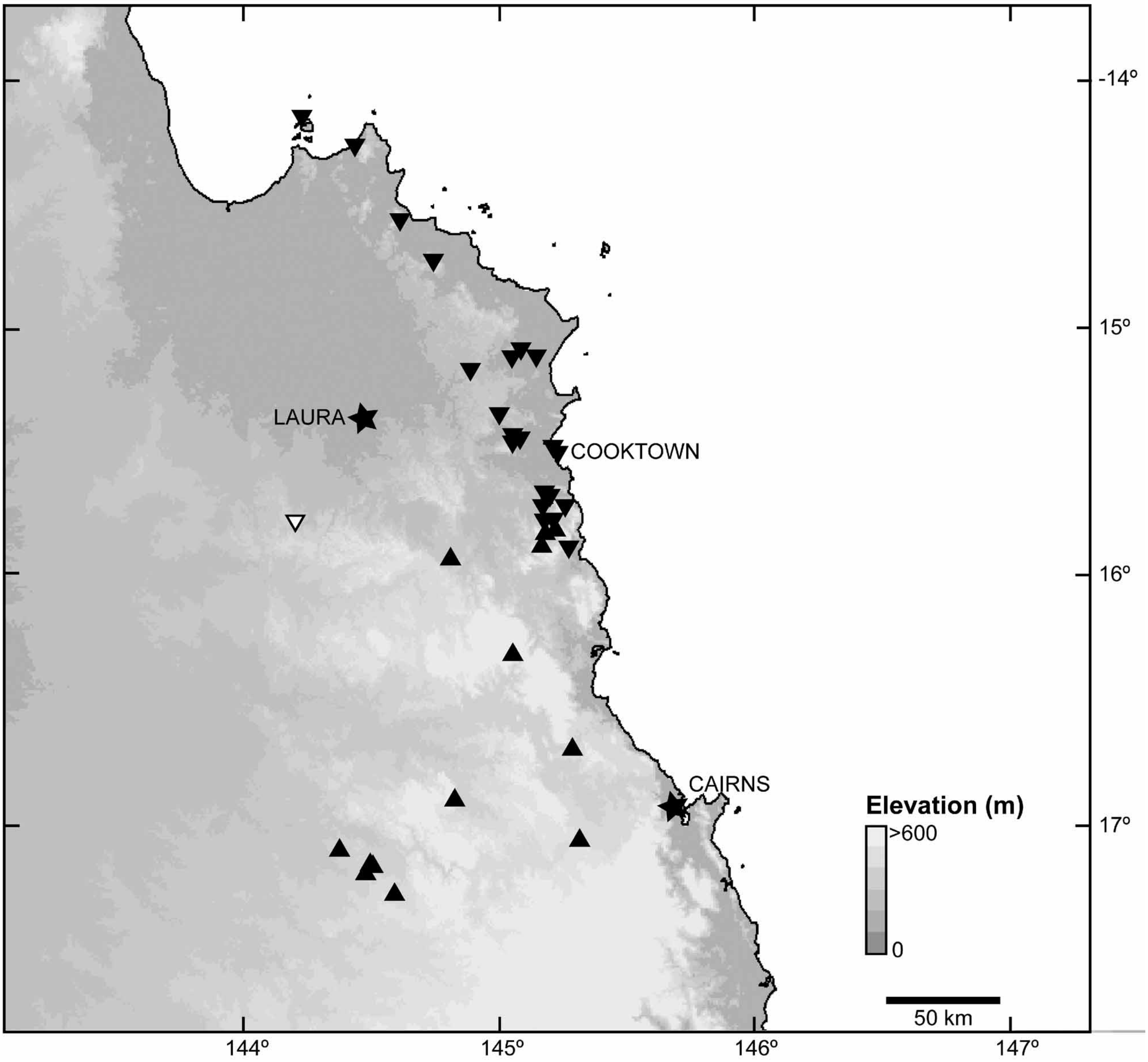

FIGURE 15. Distribution of *Cyrtodactylus tuberculatus* (inverted triangles) and *C. mcdonaldi* (upright triangles). Open symbol indicates photographic record only.

The Bloomfield River specimens (AM R2250–51) are typical *C. tuberculatus*, but are nominally from a locality that overlaps latitudinally with *C. mcdonaldi* n. sp. These two specimens were presented, as part of a larger collection of local reptiles, by George Hislop (1839–1909), who lived at Wyalla on the Bloomfield River, according to a contemporary account (Anon 1887). The flat area just north of the Bloomfield River mouth is now Wyalla Plains, crossed by Hislop's Creek. Hislop's property was on the track north of the Bloomfield River to the Mt Romeo tin-fields, and he was well-known to the workers at the tin-fields (Anon 1887). Hence, the track referred to is presumably the Grass Tree Pocket Road, which passes through Stuckey's Gap. The track from Wyalla to Mt Romeo passed near Mt McMillan, which Hislop was known to have visited (Anon 1887), and he would have obtained his supplies and shipped his collection from Cooktown. Hence, it is possible that he obtained the specimens from north of his property. We regard the "Bloomfield River" locality as an approximation only, and have provided coordinates for the Wyalla Plains rather than the current settlement at Bloomfield River.

In addition to the distribution based on examined specimens, Hoskin and Higgie (2008) report "*Cyrtodactylus louisiadensis*" from Jowalbinna Station, south-west of Laura, about 110 km west of the southern end of the distribution of *C. tuberculatus*. We have examined photographs, and tentatively identify the species at that locality as *C. tuberculatus*.

The Rockhampton locality reported by Barbour (1921) is well outside the known distribution of Australian *Cyrtodactylus*. The specimen is a typical *C. tuberculatus*, and the locality is here considered erroneous. Even further distant is the nominal locality for AM R16905, Point Lookout, NSW. This specimen is identified in the registration entry as *Phyllurus cornutus* (Ogilby 1892) (material of that nominal species from that locality is now *Saltuarius moritzi* Couper *et al*. 2008), and given this identification, it is assumed that the tag has subsequently become associated with the wrong specimen.

Conservation status. Using the IUCN criteria, this species most closely fits the Least Concern category (LC), in that it has a relatively large distribution with little evidence of continuing declines or fluctuations and with extensive parts of its distribution in protected areas.

Comments. Although Wells (2002) stated that *C. tuberculatus* can attain a maximum body length of around 160 mm, we have found no evidence of such extreme sizes among the material available to us of this species in the sense used by Wells (populations between the Atherton Tableland and the Cooktown area), or indeed in any Australian *Cyrtodactylus* population. Given that our samples are sexually mature by 91 mm for females (QM J60620) and 97 mm for males (QM J54127, J87034), and the next smallest individuals (QM J24493, 82 mm; AM R57123, 79 mm, both females) are immature and not approaching maturity, we estimate maturity is reached at about 90 mm. A hypothetical maximum SVL of 160 mm would provide a ratio of maximum/minimum mature sizes of 1.78, beyond that known for other gekkonines (1.26–1.30 for males, 1.13–1.21 for females for two *Cyrtodactylus* species; Fitch 1981; 1.03–1.44 for males of nine other gekkonine species and 1.01–1.29 for females of eleven other gekkonines; Doughty 1996; Doughty & Thompson 1998; Fitch 1981, excluding the South American species of *Phyllodactylus* Gray 1828 listed by Fitch from the data of Dixon and Huey 1970, which included subadults in the range). Using the maximum sizes in our material, the ratios were 1.29 (males) and 1.33 (females) for *C. tuberculatus*.

Specimens examined. AM R2550–51, Bloomfield River, Cooktown (15º 52' S 145º 19' E), R3953, R80529, Cooktown (15º 28' S 145º 15' E), R16905, "Point Lookout, NSW" (in error), R18501, Mt Amos (15º 42' S 145º 18' E), R56946, 40 km NW Cooktown (15º 20' S 145º 02' E), R57123, Helenvale rainforest site 28 (15º 42' S 145º 13' E), R81899–900, Cooktown district (15º 28' S 145º 15' E), AMNH 69548–49, Bowie Spur, Black Mountain (15º 40' S 145º 13' E), 120272–74, Black Gap, 20 km S, 3 km W Cooktown, 90-120 m (15º 39' S 145º 13' E), MCZ 6470, Cooktown (holotype of *Gymnodactylus olivii*) (15º 28' S 145º 15' E), 7829, "Rockhampton" (in error), 112190, Black Mountain, 13 mi. S, 2 mi. W Cooktown (15º 39' S 145º 13' E), 112191, Mungumby Creek, 16 mi. S Cooktown, 500' (15º 42' S 145º 12' E); MV D7874, Endeavour River (holotype of *Hoplodactylus tuberculatus*), D66983, D66991, D66997, D68135–37, Endeavour River, 14.5 km W, 3.2 km N Cooktown (15.423000º S 145.1178333º E); QM J17512, 19.2 km W Cooktown (15º 26' S 145º 05' E), J23328, 13 km W Cooktown (15º 25' S 145º 05' E), J24493, 20.8 km W Endeavour River, Cooktown (15º 26' S 145º 07' E), J27083, Mt Cook, S Cooktown (15º 30' S 145º 16' E), J27256, 12 Mile Scrub, 30 km S Cooktown (15º 46' S 145º 13' E), J51108, 9 km SE Mt Webb NP (15º 06' S 145º 11' E), J52850, J60620, J60622, Black Mountain, via Cooktown (15º 40' S 145º 14' E), J53634, Black Mountain, nr Helensvale (15º 41' S 145º 14' E), J54127, Black Mountain, via Cooktown (15º 41' S 145º 14' E), J60319, Mt Webb (15º 04' S 145º 07' E), J60328, Stanley Island, Flinders Group (14º 08' S 144º 15' E), J60601, Rocky Point, 6 km ENE Saddle Hill (14º 43' S 144º 46' E), J60607, Altanmoui Range, Cape Melville (14º 33' S 144º 38' E), J60621, J78295, Black Mountain, via Cooktown (15º 39' S 145º 13' E), J60862, J60867, J60869, Cape Melville NP (14º 15' S 144º 27' E), J87009, J87034–38, Black Mountain, via Cooktown (15º 38' 54" S 145º

13' 08" E), J87010, Jensen's Crossing, Endeavour River (15º 07' 06" S 145º 07' 06" E), J87022–25, Finch Bay, Cooktown (15º 28' 17" S 145º 15' 42" E), J87026–31, Byer's Creek, Mt Leswell (15º 45' 26" S 145º 15' 08" E), J87188–89, Glenrock, 2 km W McIvor River crossing (15º 06' S 145º 05' E), J88586–87, J88593, J88595, Bridge Creek National Park (15º 09' 07" S 144º 55' 05" E), J88591, Bridge Creek National Park (15º 09' 11" S 144º 55' 02" E), J88598, Bridge Creek National Park (15º 09' 07" S 144º 55' 10" E), SAM R12058, R14002, Cooktown (15º 28' S 145º 15' E).

Comparison with other species. *Cyrtodactylus tuberculatus* differs from *C. klugei* and *C. robustus* in having many fewer femoroprecloacal pores (34–44 *vs* 66 or more; Kraus 2008) in males. The difference in number of pores is mirrored by the number of scales bearing them, which are countable in both males and females (34–46 *vs* 69–92), and by the number of transventral scales (24–37 *vs* 41–54; counts from this study, which differ slightly from those provided by Kraus 2008, possibly reflecting different reference points). *Cyrtodactylus tuberculatus* is much more strongly tuberculate than *C. klugei.* It is further distinguished from *C. klugei* in having three or more dark bands across the trunk (*vs* usually two), head dorsum marbled (*vs* immaculate), and in usually possessing dark macules in the pale interspaces between bands (*vs* always lacking). It is further differentiated from *C. robustus*, with which it shares very prominent tubercles, in its lesser size (SVL to 119 mm *vs* 161 mm; Kraus 2008), presence of a dark band across the hips (*vs* usually lacking), and marbled lips (*vs* pale lips). It also lacks the bright orange cloaca of *C. robustus*.

For comparison with other Australian *Cyrtodactylus*, see the descriptions of those species.

Natural history. This species has been collected from the granite boulder fields at Cape Melville (Keith McDonald, pers. comm.). It is found on sandstone at Isabella Falls and Bridge Creek (near Cooktown) and sheltering in the extensive aerial root systems of mature fig trees (*Ficus virens*) in riverine rainforest along the banks of the Endeavour River. It will also colonise buildings in the Endeavour Valley that are in close association with suitable habitat. At Finch Bay (Cooktown) it was found amongst large granite boulders on the beach front that were backed by open eucalypt forest with rainforest emergents. At Black Mountain (Fig. 16A), it is generally associated with the vegetation on the basal slopes (*Ficus virens, Ficus obliqua,* eucalypts and umbrella trees) but a juvenile was found at night well up on the boulder field. At this locality, it can also be seen during the day sheltering in the cavities beneath granite boulders near the base of the mountain. Specimens collected at Mt Leswell came from granite boulders and vegetation along a drainage line.

Observations on feeding by this species, together with stomach content records are provided by Covacevich *et al*. (1996), although their data combine records of several species following this revision. The records specifically based on *C. tuberculatus* are of predation on the frog *Litoria pallida* and the gecko *Nactus galgajuga,* and stomach contents of seven individuals comprising unidentified arachnids (n = 2 stomachs), unidentified Orthoptera, Orthoptera (family Gryllacrididae), Blattodea (Family Blaberidae, *Calolampra* sp.), Hymenoptera (family Formicidae, queens of *Oecophylla smaragdina*), and Coleoptera (family Elateridae).

Cyrtodactylus mcdonaldi sp. nov.

Figs. 17–18

Holotype. QM J87075, female, The Archways Cave section, Chillagoe–Mungana Caves National Park, 350 m above sea level (asl) (17º 05' 29" S 144º 23' 28" E) (P. Couper & K. McDonald, 28.ix.2008).

Paratypes. MCZ 152021, Laura River, Cook Hwy, 2 [28] mi. W, 32 mi. S Cooktown (15º 55' S 144º 50' E); QM J19327, Mt Molloy (16º 41' S 145º 20' E); J30062–63, 21.4 km E Chillagoe (17º 16' S 144º 37' E); J31272, J48084, Chillagoe (17º 09' S 144º 31' E); J45365, Mt Mulligan (16º 53' S 144º 51' E); J60725–26, Little Forks, Annan River (15º 49' S 145º 13' E); J61772–73, nr Chillagoe township (17º 09' S 144º 31' E); J63482, Windsor Tableland (16º 18' S 145º 05' E); J87047–48, Ship Rock, Mt Poverty, Grey Range (15º 51' 47" S 145º 12' 19" E); J87070, Mt Windsor National Park (16º 18' 06" S 145º 05' 25" E); J87071, Donner Cave, Chillagoe–Mungana Caves National Park (17º 09' 57" S 144º 30' 57" E); J87072–74, 87076–77, The Archways Cave section, Chillagoe–Mungana Caves National Park (17º 05' 29" S 144º 23' 28" E); J87078, Granite Gorge, via Wakamin (17º 02' 50" S 145º 21' 15" E); J87083, Royal Arch Tower section, Chillagoe–Mungana Caves National Park (17º 11' 06" S 144º 29' 57" E); J87084, Royal Arch Tower section, Chillagoe–Mungana Caves National Park (17º 11' 00" S 144º 29' 51" E); J88027–88028, Parrot Creek Falls, via Shiptons Flat (15º 48' 08" S 145º 15' 24" E).

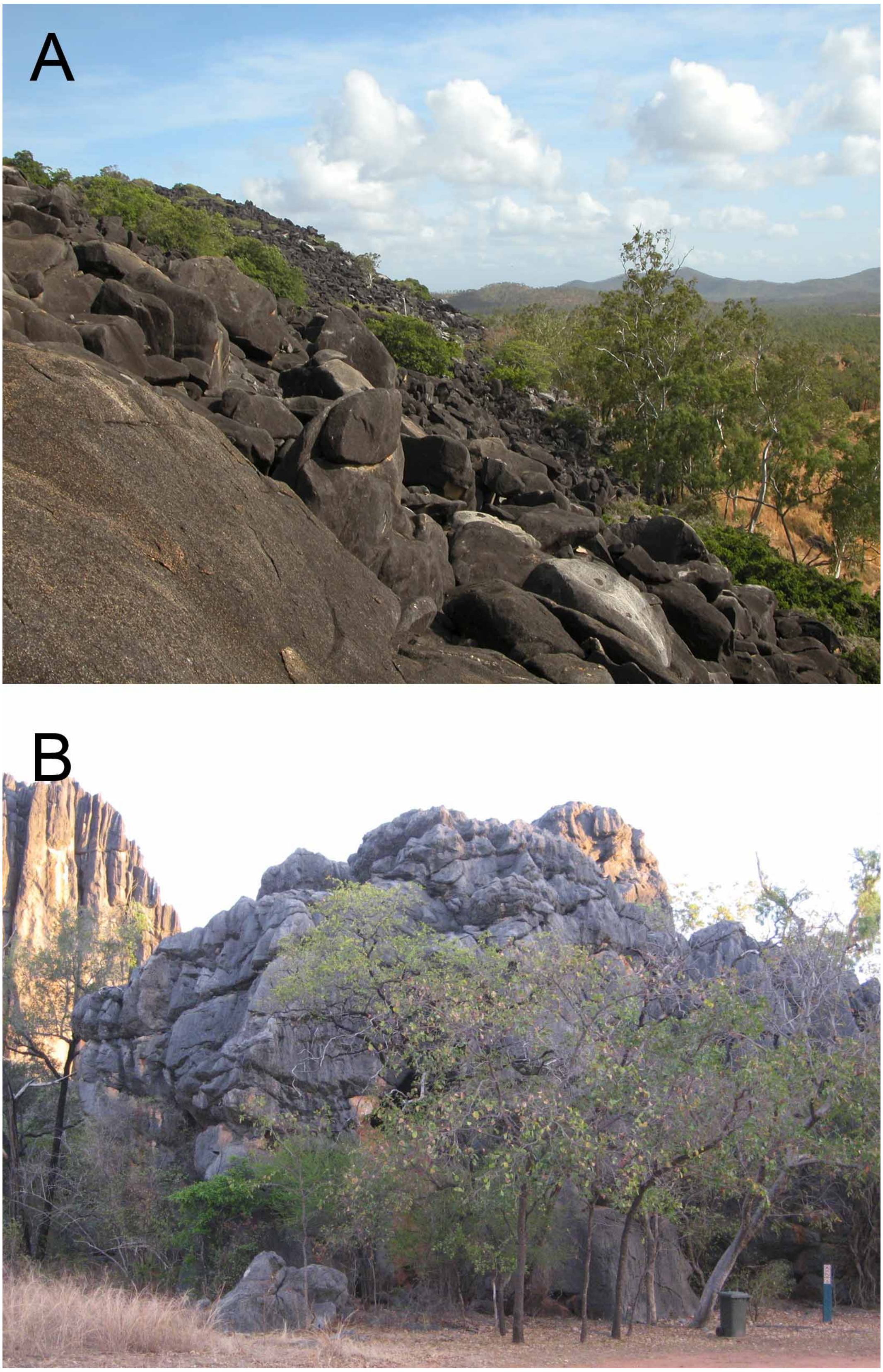

FIGURE 16. Habitats of A. *Cyrtodactylus tuberculatus* at Black Mountain, Qld (Photo: A. Amey) and B. *C. mcdonaldi* at Chillagoe, Qld (Photo: P. Couper).

FIGURE 17. Holotype of *Cyrtodactylus mcdonaldi* (QM J87075).

FIGURE 18. *Cyrtodactylus mcdonaldi* from Chillagoe, Qld, in life (Photo: S. Wilson).

Diagnosis. A medium-sized *Cyrtodactylus* (SVL to 105 mm) with large, weakly to moderately projecting tubercles on antebrachium, strongly developed dorsal tubercles in 18–23 longitudinal rows at the midpoint of the trunk (axilla-groin interval), 28–41 ventral scale rows at the same level, a continuous series of 34–46 enlarged femoroprecloacal scales extending from one knee to the other, in males, pores are in three sections with 4–9 unpored scales between; mental with a posterior extension extending between postmentals; lips marbled or stippled with brown, dark dorsal bands on trunk usually three, with a narrow dark edge posteriorly but usually not anteriorly; pale interspaces between dark body bands usually unspotted, rarely with a few dark macules; basal tail bands only a little wider than pale interspaces.

Description. Size medium (males 69.5–95 mm, mean = 85.6 mm, sd = 8.19, n = 7; females 36–105 mm, mean = 90.1 mm, sd = 15.34, n = 19).

Head relatively long (HL/SVL 27.9–34.1%, mean = 29.9%; sd = 1.58, n = 25) and wide (HW/HL 63.6–78.8%, mean = 70.5%; sd = 3.62, n = 25), moderately depressed (HD/HL 35.8–43.4%, mean = 40.7%, sd = 1.95, n = 25), distinct from neck. Loreal region moderately inflated, canthus rostralis poorly defined. Interorbital region and top of snout concave, deepest and widest just anterior to level of rostral canthus of eye. Snout moderately long (SL/HL 28.4–41.0%, mean = 37.2%, sd = 2.19, n = 25; only one individual less than 35.1%); EN/HL 25.2–30.0%, mean = 27.6%, sd = 0.98, n = 25), much longer than eye diameter (SL/EYE 118.3–193.0%, mean = 167.8%, sd = 15.99, n = 25, only one less than 143.6%), and a little longer than eye-ear interval (EE/HL 27.6–33.1%, mean = 29.9%, sd = 1.42, n = 25). Eye large (EYE/HL 19.2–27.0%, mean = 22.3%, sd = 2.03, n = 25), pupil vertical with crenated margin, forming about 3–4 low lobes along each edge of pupil. Supraciliaries in a double row, large, frill-like, well-differentiated from adjacent more medial granules of the brow ridge, and largest anteriorly. Ear opening small (EAR/HL 6.7–12.3%, mean = 8.8%, sd = 1.21, n = 25), usually a little taller than long and slightly angled posterodorsally, but sometimes rounder. Rostral wider than high, height at centre less than that more laterally, dorsal part usually divided by a relatively straight median groove (groove with small side branch in QM J87078, 'T'-shaped in QM J87072, terminates as a small isolated scale within the rostral shield in QM J60726 and replaced by a small scale deeply penetrating the upper medial edge of the rostral in QM J87047) that extends approximately ½ the midline height of the scale, and fails to reach the oral margin. Usually two enlarged supranasals separated by usually a single, less enlarged internasal (supranasals in contact in QM J87076 and QM J87084, and two internasals present in QM J87048). External nares circular, bordered by first supralabial, rostral, supranasal, nasal (extending into posterior part of nostril) and 1–3 smaller granular scales between nasal and first supralabial. Nares moderately separated (IN/HL 10.9–15.6%, mean = 12.5%, sd = 0.91, n = 25). Supralabials anteriorly large, distinct from adjacent loreal granules, 8–10 (mode = 8 (48.0%), mean = 8.7, sd = 0.75, n = 25) to level of mid-orbit, then inflecting dorsally and posteriorly, and becoming smaller, to gradually blend along rictal margin with adjacent small granules; supralabials separated from orbital margin by at least two rows of small granular scales at narrowest point. Mental wider than deep, with a strong median extension, a little to moderately narrower (50% of specimens) or equal to rostral, and bordered posteriorly by a single elongate pair of large postmentals (Fig. 10B). Infralabials anteriorly much larger than adjacent gular scales, becoming smaller posteriorly, 8–12 (mode = 10 (44.0%), mean = 9.8, sd = 0.82, n = 25). First infralabial with ⅔–¾ of ventral border contacting postmental, ¼ –⅓ by anteriormost enlarged subinfralabial (fully contacting postmental in QM J87072 and QM J87084). Subinfralabial scales anteriorly large, flattened, and polygonal, becoming smaller, more rounded and granular posteriorly and medially (towards gular area).

Body moderately robust (AGL/SVL 33.5–47.1%, mean = 42.2%, sd = 2.82, n = 25), with low, but distinct, ventrolateral skin folds approximately marking the transition between the enlarged flattened ventral scalation and the smaller, more rounded, granular lateral scalation. Scales on dorsum of head, body and limbs small, juxtaposed, rounded granules, with interspersed much larger tubercles. Granular scales finest over parietal region of head, becoming coarser over body, then more polygonal and flatter on tail. On head dorsum, tubercles small and only slightly projecting, anteriorly commencing in the posterior interocular area, becoming larger, more projecting and with a more conical, slightly posteriorly-tilted apex over nape (Fig. 11B). Tubercles on body dorsum larger again (Fig. 12B), but with a more longitudinally ovoid base, often with a weak median keel, and relatively low on anterior body, but becoming much more projecting posteriorly on body, over sacrum and onto tail base, where they are markedly conical. Tubercles persist along tail, one to two whorls per segment, becoming lower and less differentiated until eventually losing their distinction by about the fifth dark band. Large tubercles on body dorsum separated by 2-4 smaller granular scales, those on head and nape more widely separated by several scales. Tubercles on body arranged in about 18–23 (mean = 20.5, sd = 1.36, n = 25) roughly longitudinal rows. Dorsum of brachium relatively homogenous, sub-imbricate to imbricate; antebrachium with more imbricate, larger scales distally and over manus, and with dispersed, larger tubercles (Fig. 13B). Dorsum of thigh and crus with small, juxtaposed granules and densely packed, large tubercles, only dorsum of pes with imbricate scales (Fig. 13G).

Laterally, tubercles commence over temporal region and in postinfralabial area, where they are noticeably larger (Fig. 11G) than those of the head dorsum, then along nape and body, where they are smaller and noticeably less protuberant than those dorsally, and along tail, commencing on tail base as prominent, protuberant, conical scales, then rapidly losing differentiation by second dark tail band (Fig. 14B).

Ventrally, gular scales small, rounded and juxtaposed, becoming larger, flat and more imbricate over body venter, from clavicular region. Ventral scales at midbody, between ventrolateral skin folds 28–41 (mean = 34.4, sd = 3.74, n = 26). Ventral scales on brachium and antebrachium like gular scales. On ventral surface of thighs, but not on crus or in precloacal region, an abrupt junction between enlarged imbricate scales and much smaller scales posteriorly, enlarged scales 37–45 between distal extent on each thigh (mean = 41.7, sd = 2.37, n = 26). Ventral scales of tail base like those of body, most of tail venter with a single median series of very broad scales about four times the width of adjacent ventrolateral scales.

Precloacal and femoral pores present in males, separated by unpored scales into three patches. Distal femoral pores 8–11 (mean = 8.9, sd = 0.67, n = 14), separated by 4–9 unpored scales (mean = 6.7, sd = 1.32, n = 14) from the 13–16 (mean = 13.9, sd = 1.46, n = 7) proximal femoral + precloacal pores. Unilaterally on three individuals, a single pored scale located within the unpored series, towards its distal end.

Pores best developed in precloacal region where they are deep and transversely oriented, becoming much shallower, smaller and rounder distally under thigh. No pubic groove. About three large blunt-tipped postcloacal spurs on ventrolateral surface of tail base, more projecting in adult males than females or juveniles.

Forelimbs and hindlimbs well-developed (FLL/SVL 14.0–16.9%, mean = 15.3%, sd = 0.88, n = 25; HLL/SVL 16.5–19.2%, mean = 17.9%, sd = 0.72, n = 25). Digits well-developed, reflected dorsally at proximal interphalangeal joint, and all bearing robust, strongly curved claws sheathed at the base by two scales. Subdigital lamellae expanded basally, beginning on pes over distal part of metatarsals and ending at point of reflection of toes, lamellae distal to this point not expanded. Lamellae under first toe 5–9 expanded (mean = 7.1, sd = 0.95, mode = 7 (48.0%)) + 8–11 narrow (mean = 9.0, sd = 0.73, mode 9 (60.0%)), total 13–18 (mean = 16.1, sd = 1.17, mode = 16 (48.0%), n = 25). Lamellae under second toe 7–10 expanded (mean = 8.5, sd = 0.82, mode = 9 (44.0%)) + 8–11 narrow (mean = 9.8, sd = 0.78, mode = 10 (48.0%)), total 16–20 (mean = 18.2, sd = 0.97, mode = 18 (40.0%), n = 25). Lamellae under third toe 7–12 expanded (mean = 9.5, sd = 1.12, mode = 9 (36.0%)) + 9–12 narrow (mean = 10.8, sd = 0.90, mode = 11 (44.0%)), total 17–23 (mean = 20.3, sd = 1.38, mode = 21 (48.0%), n = 25). Lamellae under fourth toe 8–13 expanded (mean = 11.1, sd = 1.50, mode = 12 (48.0%)) + 10–13 narrow (mean = 11.0, sd = 0.87, mode = 11 (52.0%)), total 19–25 (mean = 22.1, sd = 1.41, mode = 23 (36.0%), n = 25). Lamellae under fifth toe 7–10 expanded (mean = 8.6, sd = 0.76, mode = 8 (44.0%)) + 10–13 narrow (mean = 11.4, sd = 0.96, mode = 12 (40.0%)), total 18–22 (mean = 20.0, sd = 1.06, mode = 20 (40.0%), n = 25). Relative lengths of digits on manus I<II<V<III<IV; on pes I<II<III=V<IV. Very slight traces of webbing between bases of fingers; weak webbing between bases of toes 2–3, 3–4 and 4–5.

Tail a little longer than body (TL/SVL 117.0–128.7%, mean = 123.6%, sd = 4.40, n = 5), narrow at base (TW/SVL 5.8–11.1%, mean = 7.8%, sd = 1.24, n = 25) and tapering evenly to a conical tip. Tail segments externally identifiable by straight scale junctions, segments about 7–9 scales long when counted to include tubercles. Cloacal sacs present in both sexes, larger in males, external orifices just posterior to vent, laterally.

Colour in preservative. Dorsal pale ground colour fawn. Head dorsum (Fig. 11B) without brown mottling and bordered posterolaterally by a fine pale edge. Pale nape zone bordered posteriorly by a U-shaped mid to dark brown chevron on nape, widest vertebrally, and extending anteriorly over temporal region to eye, then visible as a narrowing, increasingly diffuse streak over the lores to the nostril. Second broad dark transverse dorsal band over shoulders, lateral margins extending more narrowly anteroventrally in front of forelimbs. Three dark bands over trunk, extending lateroventrally with even width, but dissipating over flanks. A dark band over hips in 54% of specimens (n = 26), a pale band in 46%. Tail with dark bands over most of length which become paler and less defined near the tip. When they can be counted to the distal end of tail, dark tail bands 10–14 (mean = 11.7, sd = 1.30, n = 12). On nape and body, dark bands usually somewhat wider than pale interspaces, and with abrupt straight edges; pigmentation darkest along the posterior margin but sometimes a darker edging is also evident along the anterior edge. Bands on tail (Fig. 14B) of similar width to body bands, and usually significantly wider than pale interspaces, but darker and more solidly dark than those of body. Pale interspaces on body generally clean.

Upper and lower lips (Fig. 11G) cream, finely stippled with brown or with brown mottling. Dorsum of forelimbs and hindlimbs usually with little indication of pattern, although obscure bars are sometimes present on the thighs.

Entire ventral surface usually immaculate cream, including the underside of the tail. Some specimens with diffuse brown mottling which is strongest in the gular region.

Description of holotype. The holotype of *C. mcdonaldi* is a mature-sized female, with the following character states of those variable for the taxon: SVL 100 mm, AGL 45 mm, TL 125 mm, TW 8.0 mm, HL 28.0 mm, HW 21.1 mm, HD 11.7 mm, IN 3.4 mm, SL 10.6 mm, EN 7.9 mm, EYE 5.7 mm, EE 9.0 mm, EAR 2.4 mm, FLL 15.3 mm, HLL 18.4 mm, lamellae below digits I–V 8+9, 10+9, 10+11, 12+11, 9+10 respectively, supralabials 10, infralabials 10, rows of dorsal tubercles 20, transventral rows 34, femoroprecloacal scales 43, dark band across hips present and dark tail bands 12.

Etymology. Named after Keith R. McDonald (b: 1950), Principal Senior Technical Officer, Threatened Species Unit, Queensland Department of Environment and Resource Management, and an Honorary Research Associate of the Queensland Museum, resident of Atherton, and discoverer of numerous north Queensland reptile and amphibian species. It was Keith who first alerted PC that Australian '*C. louisiadensis*' had an interesting, fragmented distribution and warranted further investigation. Keith was instrumental in collecting many of the initial tissue samples on which this revision is based.

Distribution. From Parrot Creek Falls, near Shiptons Flat, in the north, south to Chillagoe and 21.4 km E Chillagoe (Fig. 15).

Conservation status. Using the IUCN criteria, this species most closely fits the Least Concern category (LC), in that it has relatively large distribution with little evidence of continuing declines or fluctuations and with extensive parts of its distribution in protected areas.

Comparison with other species (Table 6). *Cyrtodactylus mcdonaldi* is geographically proximate to *C. tuberculatus* with the two closest localities for each species (Mt Leswell *C. tuberculatus* and Parrot Creek Falls *C. mcdonaldi*) being separated by only 3 km. *Cyrtodactylus mcdonaldi* is also a sister taxon of *C. tuberculatus* with an average sequence divergence of 11.07% (Table 2). It may be differentiated morphologically from *C. tuberculatus* by males having the distal femoral pores separated from the proximal femoroprecloacal pores by 4–9 unpored scales. It is further differentiated from *C. tuberculatus* by its smaller size (SVL males 69.5–100 *vs* 96–116.5 mm; females 88.5–105 *vs* 46–119 mm), less tuberculate skin (most obvious in the postlabial area, which is smooth *vs* usually tuberculate in *C. tuberculatus*, and on the antebrachium, which has protruding tubercles only on the largest individuals, but flat tubercles often present *vs* strongly projecting tubercles in all adult *C. tuberculatus*). The colour pattern is generally 'cleaner' than in *C. tuberculatus*, with the crown of the head only with grey smudges (*vs* usually strongly mottled), the labial areas less strongly mottled, the postlabial area usually immaculately pale (*vs* mottled), the pale interspaces between dark body bands lacking dark macules (*vs* usually with some dark spots), and the antebrachium nearly plain (*vs* usually more mottled). The dark body bands usually have only a prominently dark posterior margin (both prominent dark anterior and posterior edges in *C. tuberculatus*). A dark band over the hips is often lacking in *C. mcdonaldi*, but consistently present in *C. tuberculatus*.

Cyrtodactylus mcdonaldi differs from *C. klugei* and *C. robustus* in having many fewer femoroprecloacal pores (29–35 *vs* 66 or more; Kraus 2008) in males. The difference in number of pores is mirrored by the number of enlarged scales bearing them, which are countable in both males and females (37–45 *vs* 66 or more), and by the number of transventral scales (28–41 *vs* 41–54). It differs from both in having the femoroprecloacal pores broken into three series. *Cyrtodactylus mcdonaldi* is much more strongly tuberculate than *C. klugei*. It is further distinguished from *C. klugei* in having three dark bands across the trunk (*vs* usually two). It is further differentiated from *C. robustus*, with which it shares prominent tubercles, in its lesser size (SVL to 105 mm *vs* 161 mm; Kraus 2008), presence of a dark band across the hips (*vs* usually lacking), and marbled lips (*vs* pale lips). It also lacks the bright orange cloaca of *C. robustus*.

For comparisons with *C. hoskini*, *C. adorus* and *C. pronarus*, see the descriptions of those species.

Natural history. At Chillagoe, this species is found around limestone karsts, associated with poorly developed vine thickets, in open savannah woodland (Fig. 16B). A specimen from the Mareeba area was collected from an isolated granite outcrop, in granite hill country adjacent to a drainage line, in open forest with a grassy understory. Specimens from Mt Windsor National Park came from a road cutting in granite hills, surrounded by eucalypt-dominated woodland. The Parrot Creek (Shiptons Flat) site is comprised of exposed granite along a drainage line in wet sclerophyll forest. Genetic samples from Mt Poverty were collected from animals living on granitic outcrops in tall eucalypt forest (Keith McDonald, pers. comm.). *Cyrtodactylus* (not sampled but presumably *C. mcdonaldi*) have been found in the Bloomfield area on trees in open woodland, where few rock outcrops occur (Lewis Roberts, pers. obs.). They are also known to colonise houses in this area and at Shiptons Flat (Lewis Roberts, pers. obs.).

An individual, presumably of this species, from Gap Creek via Ayton, near the Bloomfield River, was observed to catch and eat an adult gecko, *Gehyra dubia* (reported as *Gehyra australis*) on the wall of a house (Naylor 2000). Stomach contents of five individuals (J19327, J30062–63, J45365, J48084) were reported by Covacevich *et al*. (1996; as *Cyrtodactylus louisiadensis*). Seven food items were reported: the spider *Yiinthi chillagoe* (Heteropodidae), the scorpion *Liocheles* sp. (Ischnuridae), two roaches (*Laxta* sp., Blaberidae; *Methana* sp., Blattidae), two beetles (Tenebrionidae and Curculionidae), and a beetle larva, together with an unidentified nematode (possibly parasitic).

TABLE 6. Summary of variation in taxonomically important measurements and scalational characters across Australian *Cyrtodactylus* species. Data are presented as range (mean±sd) for variable characters.

Character	*tuberculatus*	*mcdonaldi*	*hoskini*	*adorus*	*pronarus*
SVL (mm)	46–120	36–105	64–112	91–123	104.5–132.5
HW/HL (%)	66.5–88.0 (75.3±5.67)	63.6–78.8 (70.5±3.62)	62.7–69.8 (67.7±2.87)	66.0–76.4 (70.5±2.97)	64.7–75.2 (68.9±2.59)
HD/HL (%)	35.3–57.5 (42.3±4.56)	35.8–43.4 (40.7±1.95)	34.0–37.1 (35.2±1.16)	34.9–54.6 (39.6±4.82)	34.4–40.0 (37.8±1.73)
EN/HL (%)	26.0–34.5 (29.3±1.72)	25.2–30.0 (27.6±0.98)	27.4–29.4 (28.4±0.76)	28.2–32.7 (29.5±1.40)	28.2–32.1 (29.8±1.09)
EE/HL (%)	25.8–36.9 (30.5±2.31)	27.6–33.1 (29.9±1.42)	23.6–27.8 (26.0±1.70)	25.2–30.0 (27.6±1.10)	26.7–30.3 (28.7±1.32)
HLL/SVL (%)	16.6–20.1 (18.2±0.82)	16.5–19.2 (17.9±0.72)	18.7–21.3 (19.6±0.95)	17.0–20.9 (18.4±0.92)	18.2–20.6 (19.0±0.60)
TL/SVL (%)	120.4–146.5 (127.9±7.73)	117.0–128.7 (123.6±4.40)	133.0–147.7 (140.4±10.4)	125.7–135.4 (131.9±4.50)	130.5–132.7 (131.6±1.56)
Dorsal tubercle rows	20–25 (22.6±1.30)	18–23 (20.5±1.36)	19–24 (21.7±1.63)	21–24 (22.6±1.18)	20–24 (22.0±1.15)
Ventrals	24–37 (31.3±2.84)	28–41 (34.4±3.74)	38–44 (39.8±2.23)	34–40 (37.0±1.71)	35–45 (40.0±2.63)
Femoroprecloacal scales	34–46 (39.8±2.69)	37–45 (41.7±2.37)	41–48 (44.5±2.74)	56–65 (60.7±2.99)	58–66 (62.1±2.54)
Femoroprecloacal pores	34–44 (38.9±2.57)	29–35 (31.0±2.16)	48	57–64 (60.9±3.02)	58–66 (62.5±2.62)
Femoroprecloacal pore row interrupted	–	+	–	–	–
Median postmental scale	–	–	–	–	+
Supralabial scales	8–11 (8.8±0.77)	8–10 (8.7±0.75)	8–10 (8.7±1.03)	9–11 (9.7±0.59)	10–12 (10.6±0.73)
Infralabial scales	8–12 (10.0±0.87)	8–12 (9.8±0.82)	9–11 (10.0±0.89)	10–12 (10.6±0.63)	11–13 (11.8±0.68)

Cyrtodactylus hoskini sp. nov.

(Figs. 19–20)

Holotype. QM J86950, female, Tozer's Gap, 205 m asl, Iron Range National Park (12º 43' 43" S 143º 11' 14" E) (P. Couper, A. Amey & L. Roberts, 15.ix.2008).

Paratypes. QM J86926–29, J86951, Tozer's Gap, Iron Range National Park (12º 43' 43" S 143º 11' 14" E).

Diagnosis. A large *Cyrtodactylus* (SVL to 112 mm) with large, moderately projecting tubercles on the antebrachium, strongly developed dorsal tubercles in 19–24 longitudinal rows at the midpoint of the trunk (axilla-groin interval); 38–44 ventral scale rows at the same level, a continuous series of 41–48 enlarged femoroprecloacal scales extending from one knee to the other, each scale bearing a pore in males; mental with a posterior extension extending between postmentals; lips marbled or stippled with brown, dark dorsal bands on trunk usually three, with a narrow dark edge anteriorly and posteriorly, and a narrow vertebral extension both anteriorly and posteriorly; pale interspaces between dark body bands usually with a grey patch or bar laterally; basal tail bands a little wider than pale interspaces.

Description. Size large (subadult male 65 mm, n = 1; females 64–112 mm, mean = 100.0 mm, sd = 20.26, n = 5).

Head relatively long (HL/SVL 27.8–33.1%, mean = 30.0%; sd = 2.32, n = 6) and wide (HW/HL 62.7–69.8%, mean = 67.7%; sd = 2.87, n = 6), moderately depressed (HD/HL 34.0–37.1%, mean = 35.2%, sd = 1.16, n = 6), distinct from neck. Loreal region moderately inflated, canthus rostralis poorly defined. Interorbital region and top of snout concave, deepest and widest just anterior to level of rostral canthus of eye. Snout moderately long (SL/HL 36.3–39.5%, mean = 38.4%, sd = 1.18, n = 6; EN/SVL 27.4–29.4%, mean = 28.4%, sd = 0.76, n = 6), much longer than eye diameter (SL/EYE 142.6–176.1%, mean = 158.9%, sd = 12.74, n = 6), and a little longer than eye-ear interval (EE/HL 23.6–27.8%, mean = 26.0%, sd = 1.70, n = 6). Eye large (EYE/HL 22.4–25.9%, mean = 24.2%, sd = 1.33, n = 6), pupil vertical with crenated margin, forming about 3–4 low lobes along each edge of pupil. Supraciliaries in a double row, large, frill-like, well differentiated from adjacent more medial granules of the brow ridge, and largest anteriorly. Ear opening small (EAR/HL 7.7–10.2%, mean = 9.0%, sd = 0.84, n = 6), usually a little taller than long and slightly angled posterodorsally, but sometimes rounder. Rostral wider than high, height at centre less than that more laterally (except in QM J86951), dorsal part divided by a straight median groove that extends about ¼–⅓ the midline height of the scale, and fails to reach the oral margin. Two enlarged supranasals separated by usually a single, less enlarged internasal (two in QM J86929) that contacts the dorsal edge of the rostral shield. External nares circular, bordered by first supralabial, rostral, supranasal, nasal (extending into posterior part of nostril) and two smaller granular scales between nasal and first supralabial. Nares moderately separated (IN/HL 12.2–13.5%, mean = 12.9%, sd = 0.45, n = 6). Supralabials anteriorly large, distinct from adjacent loreal granules, 8–10 (mode = 8 (66.7%), mean = 8.7, sd = 1.03, n = 6) to level of mid-orbit, then inflecting dorsally and posteriorly, and becoming smaller, to gradually blend along rictal margin with adjacent small granules; supralabials separated from orbital margin by at least three rows of small granular scales at narrowest point. Mental wider than deep, with a strong median extension, equal to or slightly wider than rostral, and bordered posteriorly by a single elongate pair of large postmentals (Fig. 10C). Infralabials anteriorly much larger than adjacent gular scales, becoming smaller posteriorly, 9–11 (mean = 10.0, sd = 0.89, n = 6). First infralabial with ventral border approximately ⅔ to fully contacting postmental. Subinfralabial scales anteriorly large, flattened, and polygonal, becoming smaller, more rounded and granular posteriorly and medially (towards gular area).

FIGURE 19. Holotype of *Cyrtodactylus hoskini* (QM J86950).

FIGURE 20. *Cyrtodactylus hoskini* in life. A. Tozer's Gap, Qld (Photo: P. Couper), B. William Thompson Range, Qld (Photo: K. Aland).

Body moderately robust (AGL/SVL 37.5–44.3%, mean = 41.0%, sd = 2.76, n = 6), with low, but distinct, ventrolateral skin folds approximately marking the transition between the enlarged flattened ventral scalation and the smaller, more rounded, granular lateral scalation. Scales on dorsum of head, body and limbs small, juxtaposed, rounded granules, with interspersed much larger tubercles. Granular scales finest over parietal region of head, becoming coarser over body, then larger, flatter and more polygonal on tail. On head dorsum (Fig. 11C), tubercles commence on crown area and are small, widely separated and only slightly projecting, anteriorly, becoming larger, more numerous, more projecting and with a more conical, slightly posteriorly-tilted apex over nape. Tubercles on body dorsum larger again (Fig. 12C), but with a more longitudinally ovoid base, often with a weak median keel, and relatively low on anterior body, but becoming more projecting posteriorly on body, over sacrum and onto tail base. Tubercles persist along tail, one to two whorls per segment, becoming lower and less differentiated until eventually losing their distinction by about the fourth or fifth dark band. Large tubercles on body dorsum separated by 2–3 smaller granular scales, those on head and nape more widely separated by several scales. Tubercles on body arranged in about 19–24 (mean = 21.7, sd = 1.63, n = 6) roughly longitudinal rows. Dorsum of brachium with juxtaposed small scales and relatively few larger tubercles; antebrachium with more imbricate, larger scales distally and over manus, and more numerous, large, low tubercles (Fig. 13C). Dorsum of thigh and crus with small juxtaposed granules and numerous, low, densely packed, large tubercles (Fig. 13H), only dorsum of pes with imbricate scales.

Laterally, tubercles commence over temporal region and in postinfralabial area, where they are noticeably larger than those of the head dorsum (Fig. 11H), then along nape and body, where they are smaller and similarly protuberant to those dorsally, and along tail, commencing on tail base as prominent, conical scales, then rapidly losing differentiation by third dark tail band (Fig. 14C).

Ventrally, gular scales small, rounded and juxtaposed, becoming larger, flatter and more imbricate over body venter, from clavicular region. Ventral scales at midbody, between ventrolateral skin folds 38–44 (mean = 39.8, sd = 2.23, n = 6). Ventral scales on brachium and antebrachium like gular scales. On ventral surface of thighs, but not on crus or in precloacal region, an abrupt junction between enlarged imbricate scales and much smaller scales posteriorly, enlarged scales 41–48 between distal extent on each thigh (mean = 44.5, sd = 2.74, n = 6). Ventral scales of tail base like those of body, most of tail venter with a single median series of very broad scales about four times the width of adjacent ventrolateral scales.

Precloacal and femoral pores present in males (n = 1), 48 in a single continuous row, arching shallowly anteriorly in precloacal region. No pubic groove. Usually two (three on left side of QM J86926) large, blunt-tipped, postcloacal spurs on ventrolateral surface of tail base.

Forelimbs and hindlimbs well-developed (FLL/SVL 15.5–16.5%, mean = 16.0%, sd = 0.34, n = 6; HLL/SVL 18.7–21.3%, mean = 19.6%, sd = 0.95, n = 6). Digits well-developed, reflected dorsally at proximal interphalangeal joint, and all bearing robust, strongly curved claws sheathed at the base by two scales. Subdigital lamellae expanded basally, beginning on pes over distal part of metatarsals and ending at point of reflection of toes, lamellae distal to this point not expanded. Lamellae under first toe 7–8 expanded (mean = 7.8, sd = 0.41) + 9–10 narrow (mean = 9.8, sd = 0.41), total 17–18 (mean = 17.7, sd = 0.52, n = 6). Lamellae under second toe 9–10 expanded (mean = 9.5, sd = 0.55) + 10–11 narrow (mean = 10.8, sd = 0.41), total 19–21 (mean = 20.3, sd = 0.82, n = 6). Lamellae under third toe 10–12 expanded (mean = 11.0, sd = 0.89) + 11–13 narrow (mean = 12.0, sd = 0.63), total 22–24 (mean = 23.0, sd = 0.89, n = 6). Lamellae under fourth toe 11–12 expanded (mean = 11.7, sd = 0.52) + 11–13 narrow (mean = 12.2, sd = 0.75), total 23–25 (mean = 23.8, sd = 0.98, n = 6). Lamellae under fifth toe 8–9 expanded (mean = 8.5, sd = 0.55) + 11–13 narrow (mean = 12.3, sd = 0.82), total 20–22 (mean = 20.8, sd = 0.75, n = 6). Relative lengths of digits on manus I<II<V<III<IV; on pes I<II<III=V<IV. Very slight traces of webbing between bases of fingers; weak webbing between bases of toes 2–3 and 3–4.

Tail a little longer than body (TL/SVL 133.0–147.7%, n = 2), narrow at base (TW/SVL 6.3–8.0%, mean = 7.3%, sd = 0.59, n = 6) and tapering evenly to a conical tip. Tail segments externally identifiable by straight scale junctions, segments about 7–8 scales long when counted to include tubercles. Cloacal sacs present in both sexes, external orifices just posterior to vent, laterally.

Colour in preservative. Dorsal ground colour pale grey-brown. Head dorsum (Fig. 11C) usually coarsely mottled with mid to dark brown, bordered posterolaterally by a narrow pale zone which has a poorly defined anterior edge (except in juveniles, where the anterior edge is more clearly defined). Pale nape zone bordered posteriorly by a U-shaped dark chocolate coloured chevron on nape, widest vertebrally (with a short vertebral extension both anteriorly and posteriorly) and extending anteriorly over temporal region to eye, then moderately to weakly present over posterior lores and becoming increasingly diffuse as it extends to the nostril. Second broad dark transverse dorsal band over shoulders. Three dark bands over trunk, narrowing on lateroventral surfaces and dissipating over lower flanks. Usually a dark band over hips (not present in QM J86950 and QM J86928; both specimens with a narrow dark blotch at the limb insertions, the latter specimen also has a small dark blotch on the vertebral line). Tail with dark bands over most of length, but these become increasingly obscure on the distal portion. When they can be counted to the distal end of tail, dark tail bands 13–15 (n = 2). On nape and body, dark bands usually slightly wider than pale interspaces, and with abrupt edges with a short vertebral extension both anteriorly and posteriorly; pigmentation darkest along band margins, leaving centre of bands a little lighter. Bands on tail (Fig. 14C) of similar width to body bands, and anteriorly 1½ to twice the width of the pale interspaces. Pale interspaces of body usually with a few dark smudges and some indication of a dark bar that extends dorsoventrally down the flanks.

Upper and lower lips (Fig. 11H) generally greyish-brown. Dorsum of forelimbs and hindlimbs mid-brown and mottled; in some specimens obscure darker bars are present on the thighs.

Entire ventral surface generally pale with some greyish brown mottling which is most prominent on the mental, the gular region and the jaw articulation.

Description of holotype. The holotype of *C. hoskini* is a mature-sized female, with the following character states of those variable for the taxon: SVL 107.5 mm, AGL 45 mm, TL 143 mm, TW 8.6 mm, HL 29.9 mm, HW 20.8 mm, HD 11.1 mm, IN 3.8 mm, SL 11.8 mm, EN 8.5 mm, EYE 6.7 mm, EE 8.3 mm, EAR 2.7 mm, FLL 16.9 mm, HLL 21.2 mm, lamellae below digits I–V 8+10, 10+11, 12+12, 12+12, 9+13 respectively, supralabials 8, infralabials 9, rows of dorsal tubercles 22, transventral rows 40, femoroprecloacal scales 41, dark hip band present, and dark tail bands 15.

Etymology. Named for Dr Conrad Hoskin (b. 1976) whose work on rainforest frogs and reptiles played an important role in recognizing the significance of rock landscapes (lithorefugia) in preserving ancient rainforest lineages (see Couper & Hoskin 2008); a concept that is well illustrated by the distribution of Australian *Cyrtodactylus* spp.

Distribution. The western edge of Iron Range, north Queensland (Fig. 21). In addition to the type locality, the species has been photographed in the Garraway Creek area (12º 42' 50" S 143º 10' 26" E), a locality approximately 2 km north of the type locality (C. Hoskin, pers. comm.), and from the William Thompson Range (at the point where Fall Creek drops out of the William Thompson Range, just west of the Pascoe River Crossing, 12º 55' 27" S 143º 01' 30" E; K. Aland, pers. comm.), about 29 km to the south-west (Fig. 20B).

Conservation status. This species has a very small known distribution that is unlikely to be much more extensive. We have no clear understanding of population size but expect it to be small, given the very small area of occupancy and the low genetic diversity of this species on current sampling. The large adult size and colourful pattern of this species, together with its ready collection from accessible rock outcrops, could lead to it being targeted by illegal collection from the wild for the pet trade. These factors fulfil the IUCN criteria for a Vulnerable listing (criteria D1, VU D2).

Comparison with other species (Table 6). *Cyrtodactylus hoskini* is genetically most similar to *C. tuberculatus* and *C. mcdonaldi*, differing from them by average sequence divergences of 12.12% and 11.79% respectively (Table 2). In comparison to *C. tuberculatus*, *C. hoskini* has more numerous transverse ventral scales (38–44 *vs* 24–37) and precloacal scales (41–48, mean = 44.5 *vs* 34–46, mean = 39.8), a narrower, flatter head (HW/HL 62.7–69.8% *vs* 66.5–88.0%; HD/HL 34.0–37.1% *vs* 35.3-57.5%), with a less well-developed postocular region (EN/HL 23.6–27.8% *vs* 25.8–36.9%), and is generally less tuberculate than *C. tuberculatus*, with the postlabial area barely tuberculate (*vs* strongly tuberculate), the crus with only small, low tubercles (*vs* strongly tuberculate), and caudal tubercles absent by or at the second pale band (*vs* continuing to the third or fourth pale band or more, distally). In coloration, *C. hoskini* has a generally less strongly mottled head dorsum (*vs* usually strongly mottled), strong anterior extensions of dark body bands along the vertebral line (barely present in a few individuals of *C. tuberculatus*, but usually absent), and a dark bar in the pale interspaces ventrolaterally (absent in *C. tuberculatus*, or represented by scattered rounded spots).

Cyrtodactylus hoskini has more numerous transverse ventral scales than *C. mcdonaldi* (38–44 *vs* 28–41), more numerous enlarged femoroprecloacal scales (41–48 *vs* 37–45), a longer tail (TL/SVL 133.0–147.7% *vs* 117.0–128.7%), a narrower and flatter head (HW/HL 62.7–69.8% *vs* 65.0–78.9%; HD/HL 34.0–37.1% *vs* 35.8–43.4%), with a less well-developed temporal region (EE/HL 23.6-27.8% *vs* 27.6-33.1%), and slightly longer hindlimbs (HLL/SVL 18.7–21.3% *vs* 16.5–19.2%). The subdigital lamellae counts are at the upper end of the range for *C. mcdonaldi*. The femoroprecloacal pores are in a single unbroken row (*vs* broken into three segments by unpored scales). The dark bands on body and nape have a strong anterior extension along the vertebral line (*vs* absent), the pale interspaces have a dark bar ventrolaterally (*vs* usually no dark markings), and the dark dorsal bands have strong anterior and posterior edges (usually only a pronounced dark posterior edge in *C. mcdonaldi*).

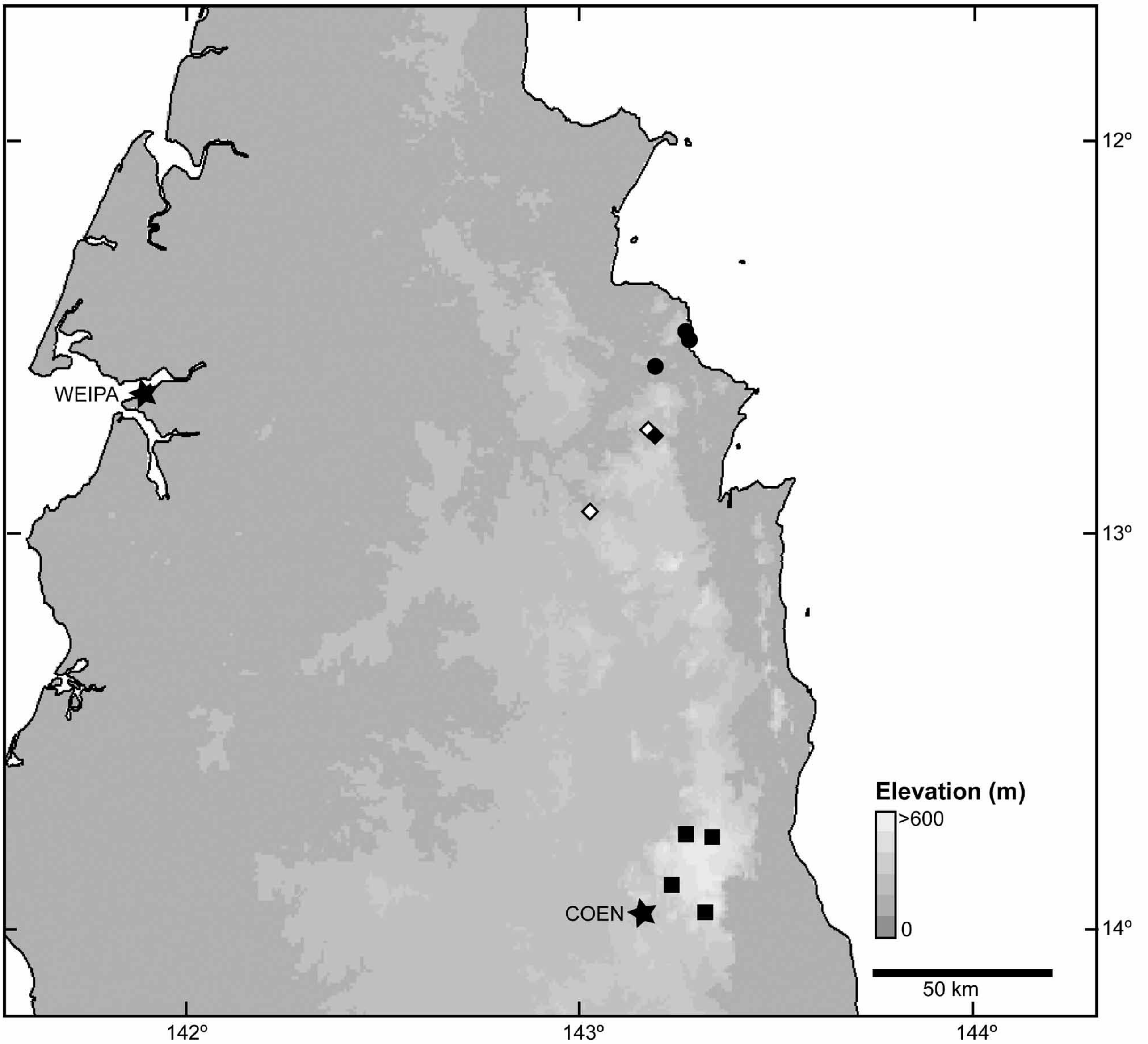

FIGURE 21. Distribution of *Cyrtodactylus hoskini* (diamonds), *C. adorus* (circles) and *C. pronarus* (squares). Open symbols indicate photographic record only.

Cyrtodactylus hoskini differs from *C. klugei* and *C. robustus* in having many fewer femoroprecloacal pores (48 *vs* 66 or more) in males. The difference in number of pores is mirrored by the number of scales bearing them, which are countable in both males and females (41–48 (*C. hoskini*) *vs* 66 or more). In comparison to *C. klugei*, *C. hoskini* has three dark bands across the trunk (*vs* usually two), and has vertebral extensions of the dark body bands (*vs* absent). It is less strongly tuberculate than *C. robustus*, is smaller (SVL to 105 mm *vs* 161 mm) and has a narrower head (HW/HL 62.7–69.8% vs 69–84%; Kraus 2008), and further differs from it in the presence of a dark band across the hips (*vs* usually lacking). It also lacks the bright orange cloaca of *C. robustus*.

For comparisons with *C. adorus* and *C. pronarus*, see the descriptions of those species.

Comments. The discovery of a *Cyrtodactylus* species at Iron Range, the stated type locality for *Cyrtodactylus abrae* Wells, 2002, requires revisiting the status of that nominal taxon. Couper *et al*. (2004) recommended treating the name as unavailable, due to the lack of a type specimen in the original description. However, if a neotype were to be designated, the name could be validated. The limited description of *C. abrae*, which appears to be based on previous accounts of a "rainforest" form of Cape York *Cyrtodactylus* presented by Wilson and Knowles (1988), in turn seemingly based on the published photograph by Cogger (1975), clearly does not represent the taxon we have described from Iron Range. Wells (2002) defined *C. abrae* as being differentiated from *C. tuberculatus* by its possession of fewer dark body bands (four, corresponding to two in our definition), and tail bands (seven). *Cyrtodactylus hoskini*, the only *Cyrtodactylus* that we have evidence of at Iron Range, has the same number of dark body bands (three) as *C. tuberculatus*, and none of the Australian *Cyrtodactylus* species have as few as seven dark tail bands or two dark body bands between axilla and groin. Wells (2002) also noted that *C. abrae* can attain a SVL of 160 mm, considerably larger than any other Australian *Cyrtodactylus*. Hence, the possibility exists that the description of *C. abrae* is based on a non-Australian taxon with incorrect type locality, and on current knowledge, it is not possible to nominate a neotype that is both from a locality close to the nominal type locality as well as according with the nominal diagnosis of the taxon. Because of the considerable risk to destabilization of nomenclature by having this name potentially become a senior synonym of any one of the numerous *Cyrtodactylus* species described since 2002 through nomination of a neotype, and the lack of sufficient detail in the description (or in the photograph provided by Cogger (1975) that seems to have been the basis for that description) to clearly assign it to any one of the numerous banded *Cyrtodactylus* species, we choose to stabilize nomenclature by nominating as neotype of *Cyrtodactylus abrae* the larger syntype of *Cyrtodactylus pulchellus*, Natural History Museum, London (BMNH) xxii.91a, from Singapore. This action accords with the sparse detail that is available in the morphological and coloration description of *C. abrae* by Wells (2002), and relegates the name to synonymy. As we have demonstrated, it is not possible to nominate a neotype that is as close as possible to the nominal type locality of *C. abrae*, consistent with Article 75.3.6 of the Code of Zoological Nomenclature (ICZN 1999), because none of the Australian *Cyrtodactylus* are morphologically consistent with the description of *C. abrae*. To comply with Article 75.3.3 and 75.3.5, relevant to validation of neotype designations, we illustrate this specimen (the larger syntype of *C. pulchellus*) in dorsal view (Fig. 22).

Natural history. The type series of *C. hoskini* was collected amongst large granite boulders in predominantly open forest interspersed with patches of rainforest (Fig. 23A). The nearby Garraway Creek site is immediately adjacent to the type locality for the microhylid frog *Cophixalus kulakula*, which is described and illustrated by Hoskin and Aland (2011) as a boulder field, with festooning ferns vines and umbrella trees. The William Thompson Range population inhabits granite boulders in outcrops and along creek and gully lines in savannah woodland that shows evidence of regular burns (K. Aland, pers. comm.).

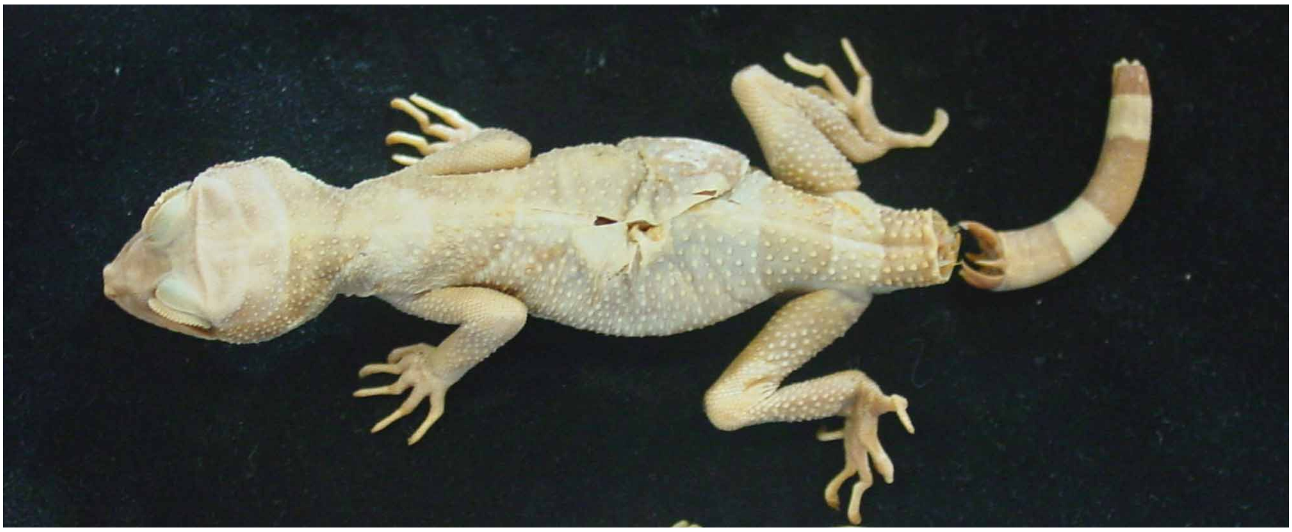

FIGURE 22. Neotype of *Cyrtodactylus abrae* — the larger syntype of *Cyrtodactylus pulchellus* (Natural History Museum London xxii.91a) (Photo: C. McCarthy).

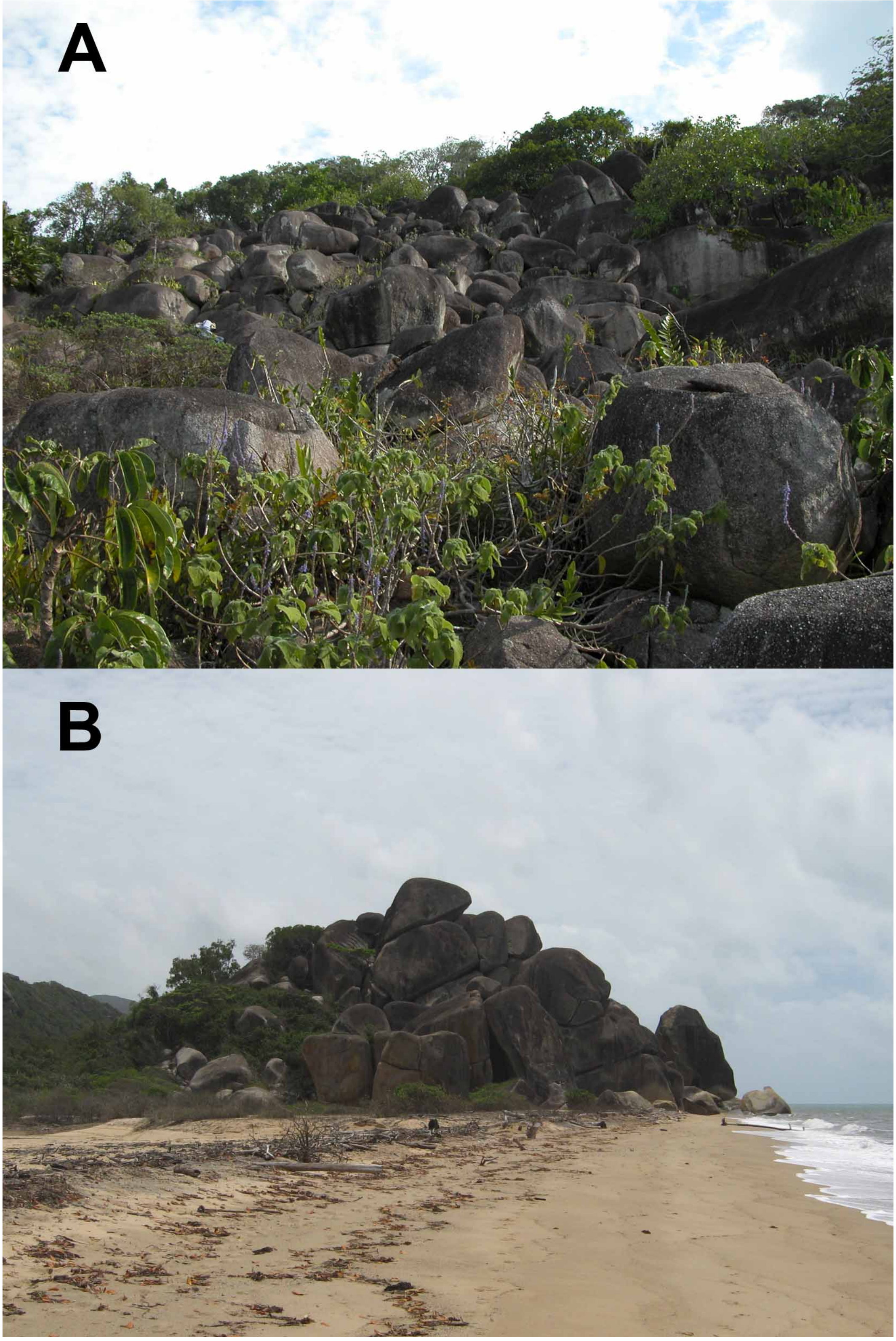

FIGURE 23. Habitats of A. *Cyrtodactylus hoskini* at Tozer's Gap (Photo: A. Amey) and B. *C. adorus* at mouth of Pascoe River (Photo: P. Couper).

Cyrtodactylus adorus sp. nov.

(Figs. 24–25)

Holotype. QM J86979, male, Pascoe River mouth, 8 m asl (12º 29' 09" S 143º 16' 28" E) (P. Couper, A. Amey & L. Roberts, 17.ix.2008).

Paratypes. QM J31806, Pascoe River (12º 30' S 143º 16' E); J86978, J86980–83, Pascoe River mouth (12º 29' 09" S 143º 16' 28" E); J86958–62, J86969, Wattle Hills (12º 32' 57" S 143º 11' 12" E); J88831–32, 2 km S Stanley Hill (12º 27' 50" S 143º 16' 14" E).

Diagnosis. A large *Cyrtodactylus* (SVL to 123 mm) with small tubercles on antebrachium, moderately developed dorsal tubercles (those over temporal region small and only slightly projecting); in 21–24 longitudinal rows at the midpoint of the trunk (axilla-groin interval); 34–40 ventral scale rows at the same level; a continuous series of 56–65 enlarged femoroprecloacal scales extending from one knee to the other, each scale bearing a pore in males; mental with a posterior extension extending between postmentals; lips cream to brown; dark dorsal bands on trunk usually three, with a narrow dark edge posteriorly, and often a narrow pale edge anteriorly, dark nape band with a narrow vertebral extension anteriorly, but other dark bands straight-edged; little or no indication of any dark marks in the pale interspaces; basal tail bands broad and evenly dark, about twice the width of pale interspaces.

FIGURE 24. Holotype of *Cyrtodactylus adorus* (QM J86979).

Description. Size large (males 91.5–119 mm, mean = 109.1 mm, sd = 9.50, n = 7; females 91–123 mm, mean = 111.8 mm, sd = 10.67, n = 8).

Head relatively long (HL/SVL 25.7–30.3%, mean = 28.2%; sd = 1.32, n = 15) and wide (HW/HL 66.0–76.4%, mean = 70.5%; sd = 2.97, n = 15), slightly depressed (HD/HL 34.9–54.6%, mean = 39.6%, sd = 4.82, n = 15, only one individual greater than 43.3%), distinct from neck. Loreal region moderately inflated, canthus rostralis poorly defined. Interorbital region and top of snout concave, deepest and widest just anterior to level of rostral canthus of eye. Snout moderately long (SL/HL 37.4–43.1%, mean = 39.5%, sd = 1.56, n = 115; EN/HL 28.2–32.7%, mean = 29.5%, sd = 1.40, n = 15), much longer than eye diameter (SL/EYE 148.6–192.3%, mean = 174.1%, sd = 10.07, n = 15), and a little longer than eye-ear interval (EE/HL 25.2–30.0%, mean = 27.6%, sd = 1.10, n = 15). Eye large (EYE/HL 20.9–26.2%, mean = 22.7%, sd = 1.51, n = 15), pupil vertical with crenated margin, forming about 3-4 low lobes along each edge of pupil. Supraciliaries in a double row, large, frill-like, well-differentiated from adjacent more medial granules of the brow ridge, and largest anteriorly. Ear opening small (EAR/HL 5.1–9.5%, mean = 7.3%, sd = 1.38, n = 15), usually a little taller than long and slightly angled posterodorsally, but sometimes rounder. Rostral wider than high, height at centre less than that more laterally (except in QM J86982), dorsal part divided by a median groove that extends about ¼–½ the midline height of the scale, and fails to reach the oral margin; the groove terminates in roughly a 'J'-shape (38% of specimens), 'T'-shape (31%), 'W'-shape (23%) or some permutation thereof, or takes the form of a widely zigzagging line (8%). Two enlarged supranasals separated by usually a single, less enlarged internasal (77% of specimens), two internasals (15%) or in direct contact (8%). External nares circular, bordered by first supralabial, rostral, supranasal, nasal (extending into posterior part of nostril) and 2–3 smaller granular scales between nasal and first supralabial. Nares moderately separated (IN/HL 11.6–14.2%, mean = 13.0%, sd = 0.66, n = 15). Supralabials anteriorly large, distinct from adjacent loreal granules, 9–11 (mode = 10 (60.0%), mean = 9.7, sd = 0.59, n = 15) to level of mid-orbit, then inflecting dorsally and posteriorly, and becoming smaller, to gradually blend along rictal margin with adjacent small granules; supralabials separated from orbital margin by at least four rows of small granular scales at narrowest point. Mental wider than deep, with a strong median extension (Fig. 10D), a little narrower to slightly wider than rostral, and bordered posteriorly by a single elongate pair of large postmentals (except in QM J86960 in which the postmentals are separated anteriorly by a small elongate scale that contacts the posterior edge of the mental and is probably a fragment of the median extension of the mental). Infralabials anteriorly much larger than adjacent gular scales, becoming smaller posteriorly, 10–12 (mean = 10.6, sd = 0.63, n = 15). First infralabial with ¾ or more of ventral margin contacting postmental (fully contacting postmental on left side of QM J86980). Subinfralabial scales anteriorly large, flattened, and polygonal, becoming smaller, more rounded and granular posteriorly and medially (towards gular area).

FIGURE 25. *Cyrtodactylus adorus* from Wattle Hills in life (Photo: P. Couper).

Body moderately robust (AGL/SVL 40.2–46.7%, mean = 42.5%, sd = 1.79, n = 15), with low, but distinct, ventrolateral skin folds approximately marking the transition between the enlarged, flattened ventral scalation and the smaller, more rounded, granular lateral scalation. Scales on dorsum of head, body and limbs small, juxtaposed, rounded granules, with interspersed much larger tubercles. Granular scales finest over parietal region of head, becoming coarser over body, then larger, flatter and more polygonal on tail. On head dorsum (Fig. 11D), tubercles small and only slightly projecting, anteriorly commencing on crown, becoming larger, more projecting and with a more conical, slightly posteriorly-tilted apex over nape. Tubercles on body dorsum larger again (Fig. 12D), but with a more longitudinally ovoid base, sometimes with a weak median keel, and relatively low on anterior body, but becoming slightly larger posteriorly on tail base, where they are more conical. Tubercles persist along tail, one to two whorls per segment, becoming lower and less differentiated until eventually losing their distinction by about the fourth dark band. Large tubercles on body dorsum separated by 2–6 smaller granular scales, as are those on the head, although tiny, and nape. Tubercles on body arranged in about 21–24 (mean = 22.6, sd = 1.18, n = 15) roughly longitudinal rows. Dorsum of brachium with slightly imbricate scalation, larger tubercles sparse to entirely absent;

antebrachium with more imbricate larger scales distally and over manus, and with numerous small tubercles (Fig. 13D). Dorsum of thigh and crus with small juxtaposed granules and densely packed larger tubercles (Fig. 13I), only dorsum of pes with imbricate scales.

Laterally, tubercles commence over temporal region (a few may be present in the postinfralabial area) where they are small and conical and only slightly larger (Fig. 11I) than those of the head dorsum, then along nape and body, where they are smaller and noticeably less protuberant than those dorsally, and along tail, commencing on tail base as prominent, protuberant, conical scales, then rapidly losing differentiation by second dark tail band (Fig. 14D).

Ventrally, gular scales small, rounded and juxtaposed, becoming larger, flat and more imbricate over body venter, from clavicular region. Ventral scales at midbody, between ventrolateral skin folds 34–40 (mean = 37.0, sd = 1.71, n = 14). Ventral scales on brachium and antebrachium like gular scales. On ventral surface of thighs, but not on crus or in precloacal region, an abrupt junction between enlarged imbricate scales and much smaller scales posteriorly, enlarged scales 56–65 between distal extent on each thigh (mean = 60.7, sd = 2.99, n = 15). Ventral scales of tail base like those of body, most of tail venter with a single median series of very broad scales about four times the width of adjacent ventrolateral scales.

Precloacal and femoral pores present in males, in a single continuous row, arching shallowly anteriorly in precloacal region. Pores 57–64 (mean = 60.9, sd = 3.02, n = 7), best developed in precloacal region where they are deep and transversely oriented, becoming much shallower, smaller and rounder distally under thigh. No pubic groove. About three large, blunt-tipped postcloacal spurs on ventrolateral surface of tail base, more projecting in adult males than females or juveniles.

Forelimbs and hindlimbs well-developed (FLL/SVL 13.4–15.7%, mean = 15.0%, sd = 0.60, n = 15; HLL/SVL 17.0–20.9%, mean = 18.4%, sd = 0.92, n = 15). Digits well-developed, reflected dorsally at proximal interphalangeal joint, and all bearing robust, strongly curved claws sheathed at the base by two scales. Subdigital lamellae expanded basally, beginning on pes over distal part of metatarsals and ending at point of reflection of toes, lamellae distal to this point not expanded. Lamellae under first toe 7–9 expanded (mean = 8.3, sd = 0.59, mode = 8 (60.0%)) + 8–12 narrow (mean = 9.9, sd = 0.96, mode = 10 (53.3%)), total 16–19 (mean = 18.2, sd = 0.77, mode = 18 (60.0%), n = 15). Lamellae under second toe 9–12 expanded (mean = 10.5, sd = 0.92, mode = 11 (40.0%)) + 10–14 narrow (mean = 11.5, sd = 0.99, modes = 11, 12 (40.0%)), total 21–23 (mean = 22.0, sd = 0.76, mode = 22 (46.7%), n = 15). Lamellae under third toe 9–13 expanded (mean = 10.8, sd = 1.15, mode = 11 (33.3%)) + 12–14 narrow (mean = 12.7, sd = 0.70, mode = 13 (46.7%)), total 22–25 (mean = 23.5, sd = 0.92, mode = 24 (40.0%), n = 15). Lamellae under fourth toe 10–14 expanded (mean = 12.1, sd = 1.10, mode = 12 (46.7%)) + 13–15 narrow (mean = 13.3, sd = 0.61, mode = 13 (73.3%)), total 23–27 (mean = 25.4, sd = 1.06, mode = 25 (40.0%), n = 15). Lamellae under fifth toe 9–11 expanded (mean = 9.5, sd = 0.74, mode = 9 (60.0%)) + 11–14 narrow (mean = 12.2, sd = 0.86, mode = 12 (66.7%)), total 21–23 (mean = 21.7, sd = 0.80, mode = 21 (46.7%), n = 15). Relative lengths of digits on manus I<II<V<III<IV; on pes I<II<III=V<IV. Very slight traces of webbing between bases of fingers; weak webbing between bases of toes 2–3, 3–4 and 4–5.

Tail a little longer than body (TL/SVL 125.7–135.4%, mean = 131.9%, sd = 4.50, n = 4), narrow at base (TW/SVL 5.5–8.8%, mean = 7.8%, sd = 0.91, n = 15) and tapering evenly to a conical tip. Tail segments externally identifiable by straight scale junctions, segments about 7–9 scales long when counted to include tubercles. Cloacal sacs present in both sexes, larger in males, external orifices just posterior to vent, laterally.

Colour in preservative. Dorsal pale ground colour greyish brown. Head dorsum (Fig. 11D) relatively unmarked, bordered posterolaterally by a narrow pale band which sometimes has a dark smudge along its anterior edge. Pale nape zone bordered posteriorly by a U-shaped dark chocolate coloured chevron on nape, widest vertebrally (with a small to moderate, rounded to pointed anterior vertebral extension) and extending anteriorly over temporal region to eye, then visible as a narrowing, increasingly diffuse streak over the lores to the nostril. Second broad dark transverse dorsal band over shoulders. Three dark bands over trunk, extending lateroventrally with even width, but dissipating over flanks. A dark band over hips. Tail with dark bands over most of length, but distal third of tail usually paler, with bands less evident. When they can be counted to the distal end of tail, dark tail bands 9–12 (mean = 11.2, sd = 1.30, n = 5). On nape and body, dark bands wider than pale interspaces, and with abrupt straight edges; pigmentation generally darkest along posterior margin of dark band and often paler along the anterior edge. Bands on tail (Fig. 14D) of similar width to body bands but wider than the pale interspaces and darker and more solidly dark than those of body. Pale interspaces of body darkest across centre, but otherwise generally unmarked.

Upper and lower lips (Fig. 11I) cream to mid-brown. Dorsum of forelimbs and hindlimbs relatively unmarked, pale to mid greyish brown.

Entire ventral surface immaculate off-white to diffusely marked with greyish brown. Generally with diffuse brown mottling on gular region and abdomen. Ventral surface of tail dark with some pale band edges visible.

Description of holotype. The holotype of *C. adorus* is a mature-sized male, with the following character states of those variable for the taxon: SVL 104.5 mm, AGL 42.5 mm, TL 141.5 mm, TW 8.7 mm, HL 30.2 mm, HW 22.2 mm, HD 11.6 mm, IN 4.0 mm, SL 12.0 mm, EN 8.9 mm, EYE 7.2 mm, EE 8.4 mm, EAR 2.5 mm, FLL 16.4 mm, HLL 21.8 mm, lamellae below digits I–V 9+10, 11+11, 12+12, 12+13, 9+12 respectively, supralabials 9, infralabials 10, rows of dorsal tubercles 21, transventral rows 38, femoroprecloacal scales 63 and dark tail bands 11.

Etymology. From the Greek άδωρος (adoros; = pure, incorruptible), alluding to the evenly and straight banded coloration, unmarred by dark spotting, curves or irregular margins.

Distribution. Known only from rocky outcrops on or near the lower reaches of the Pascoe River (Fig. 21). Wattle Hills is about 12 km upstream from the type locality near the river mouth, while the Stanley Hill site is about 2.5 km north of the type locality. The known sites are among the few rock outcrops in the area.

Conservation status. This species has a very small known distribution that is unlikely to be much more extensive and is probably also very fragmented. We have no clear understanding of population size but expect it to be small, given the very small area of occupancy and the low genetic diversity of this species on current sampling. The large adult size and colourful pattern of this species, together with its ready collection from accessible rock outcrops, could lead to it being targeted by illegal collection from the wild for the pet trade. These factors fulfil the IUCN criteria for a Vulnerable listing (criteria D1, VU D2).

Comparison with other species (Table 6). *Cyrtodactylus adorus* genetically differs from *C. tuberculatus*, *C. mcdonaldi* and *C. hoskini* by average sequence divergences of 14.28–16.43% (Table 2). Morphologically, it has many more femoroprecloacal pores (57–64 *vs* 48 or fewer) and enlarged femoroprecloacal scales (56–65 *vs* 48 or fewer) than *C. tuberculatus*, *C. mcdonaldi* and *C. hoskini*. The hindlimbs are immaculate (*vs* mottled), and the caudal dark bands are solid black (*vs* dark-edged with paler centres) and are much wider than the pale interspaces at the tail base (*vs* more nearly equal width). In comparison to all three species, *C. adorus* has much less developed tubercles, those that are present being smaller and less projecting than the other species, and the tubercles are much reduced on the tail, not reaching the third pale caudal band. In comparison to *C. mcdonaldi*, *C. adorus* has a continuous row of femoroprecloacal pores in males (*vs* broken into three segments). In comparison to the geographically closest species, *C. hoskini*, *C. adorus* also has dark dorsal bands on the body that lack vertebral extensions.

In comparison to *C. robustus*, *C. adorus* is smaller (maximum SVL 123 *vs* 161 mm), has a much more boldly contrasting and "cleaner" colour pattern, lesser development of tubercles, lacks dark speckling on the venter and orange cloacal mucosa, and has fewer dorsal tubercle rows (21–24 *vs* 24–30), transventral scales (34–40, mean = 37.0 *vs* 41–54, mean = 48.6; our counts on the type series of *C. robustus*); femoroprecloacal pores (57–64 *vs* 75–85) and enlarged femoroprecloacal scales (56–65 *vs* 75–92), and a generally narrower head (HW/HL 66–76%, mean = 71% *vs* 69–84%, mean = 77%).

In comparison to *C. klugei*, *C. adorus* is smaller (maximum SVL 123 *vs* 143 mm), has more dark body bands over the trunk (three *vs* usually two), pale lips (*vs* brown posterior supralabials), a more contrasting dorsal colour pattern, fewer transventral scales (34–40 *vs* 43–49), and fewer femoroprecloacal pores (57–64 *vs* 66–76) and enlarged femoroprecloacal scales (56–65 *vs* 69–77).

For comparisons with *C. pronarus*, see that species.

Natural history. *Cyrtodactylus adorus* was collected from a large granitic outcrop near the mouth of the Pascoe River (Fig. 23B) where it was most prevalent on rock faces in sheltered, sparsely vegetated crevices. The Wattle Hills sample came from a rocky, seasonal watercourse in monsoon forest. The Stanley Hill sample was collected on rock in deeply piled granite boulder habitat festooned with vegetation (vines, ferns, umbrella trees) (C. Hoskin, pers. comm.).

Cyrtodactylus pronarus sp. nov.

(Figs. 26–27)

Holotype. QM J86900, female, Peach Creek, 535 m asl, McIlwraith Range (13º 45' 22" S 143º 19' 59" E) (P. Couper, A. Amey, R. Howard, G. Kyle, F. Port & T. Creek, 12.ix.2009).

Paratypes. QM J38197–98, J60863–66, J60868, Peach Creek, McIlwraith Range (13º 45' S 143º 19' E); J86899, J86909–10, J86922–23, Peach Creek, McIlwraith Range (13º 45' 22" S 143º 19' 59" E); J38330–31, Lankelly Creek, McIlwraith Range (13º 53' S 143º 14' E); J60320, Klondyke Mine, McIlwraith Ranges (13º 57' S 143º 19' E).

Diagnosis. A large *Cyrtodactylus* (SVL to 132.5 mm) with enlarged tubercles on antebrachium absent, moderately-developed dorsal tubercles in 20–24 longitudinal rows at the midpoint of the trunk (axilla-groin interval); 35–45 ventral scale rows at the same level, a continuous series of 58–66 enlarged femoroprecloacal scales extending from one knee to the other, each scale bearing a pore in males; mental bordered posteriorly by a small median scale (replacing the tip of the median posterior extension of the mental), and a pair of postmentals; lips pale, strongly contrasting with the brown upper face; dark dorsal bands on trunk three, with a narrow dark edge posteriorly but the anterior margin blending with the pale interspace; pale interspaces between dark body bands lacking blotches or spots; basal tail bands more than twice as wide as pale interspaces.

FIGURE 26. Holotype of *Cyrtodactylus pronarus* (QM J86900).

Description. Size large (males 104.5–126.5 mm, mean = 119.7, sd = 7.50, n = 11; females 113–132.5 mm, mean = 125.7, sd = 9.04, n = 4).

Head relatively long (HL/SVL 27.8–30.2%, mean = 28.8; sd = 0.66, n = 16) and wide (HW/HL 64.7–75.2%, mean = 68.9%; sd = 2.59, n = 16), moderately depressed (HD/HL 34.4–40.0%, mean = 37.8%, sd = 1.73, n = 16), distinct from neck. Loreal region moderately inflated, canthus rostralis poorly defined. Interorbital region and top of snout concave, deepest and widest just anterior to level of rostral canthus of eye. Snout moderately long (SL/HL 37.7–40.9%, mean = 39.5, sd = 0.91, n = 16; EN/HL 28.2–32.1%, mean = 29.8, sd = 1.09, n = 16), much longer than eye diameter (SL/EYE 164.4–201.5%, mean = 184.6%, sd = 11.26, n = 16), and a little longer than eye-ear interval (EE/HL 26.7–30.3%, mean = 28.7%, sd = 1.32, n = 16). Eye large (EYE/HL 19.2–24.6%, mean = 21.5%, sd = 1.43, n = 16), pupil vertical with crenated margin, forming about 3–4 low lobes along each edge of pupil. Supraciliaries in a double row, large, frill-like, well-differentiated from adjacent, more medial granules of the brow ridge, and largest anteriorly. Ear opening small (EAR/HL 5.7–8.8%, mean = 7.0%, sd = 0.99, n = 16), usually a little taller than long and slightly angled posterodorsally, but sometimes rounder. Rostral wider than high, height at centre less than that more laterally, dorsal part divided by a median groove that extends about 1/6–⅔ the midline height of the scale, and fails to reach the oral margin; in 63% of specimens the median groove terminates in a small, circular scale isolated within the rostral shield (in QM J60865 the median groove extends beyond the circular scale towards the oral margin of the shield). Two enlarged supranasals separated by 1–3 less enlarged internasals that contact the dorsal edge of the rostral shield (1 = 31%, 2 = 63%, 3 = 6%). External nares circular, bordered by first supralabial, rostral, supranasal, nasal (extending into posterior part of nostril) and 2–3 smaller granular scales between nasal and first supralabial. Nares moderately separated (IN/HL 11.2–12.4%, mean = 11.8%, sd = 0.35, n = 16). Supralabials anteriorly large, distinct from adjacent loreal granules, 10–12 (mode = 10 (56.3%), mean = 10.6, sd = 0.73., n = 16) to level of mid-orbit, then inflecting dorsally and posteriorly, and becoming smaller, to gradually blend along rictal margin with adjacent small granules; supralabials separated from orbital margin by at least four rows of small, granular scales at narrowest point. Mental wider than deep and a little to moderately narrower than rostral, bordered posteriorly by a single elongate pair of large postmentals. In 88% of specimens, these are separated anteriorly by a small to moderate, elongate scale that contacts the posterior edge of the mental (Fig. 10E–F); this scale may be derived from the fragmented median extension of the rostral. Infralabials anteriorly much larger than adjacent gular scales, becoming smaller posteriorly, 11–13 (mode = 12 (50.0%), mean = 11.8, sd = 0.68, n = 16). First infralabial with ventral border ¾ to fully contacting postmental; at most only in narrow contact with anteriormost enlarged subinfralabial. Subinfralabial scales anteriorly large, flattened and polygonal, becoming smaller, more rounded and granular posteriorly and medially (towards gular area).

FIGURE 27. *Cyrtodactylus pronarus* from Peach Creek in life (Photo: K. Aland).

Body moderately robust (AGL/SVL 41.0–47.0%, mean = 44.3%, sd = 1.47, n = 16), with low, but distinct, ventrolateral skin folds approximately marking the transition between the enlarged flattened ventral scalation and the smaller, more rounded, granular lateral scalation. Scales on dorsum of head, body and limbs small, juxtaposed, rounded granules, with interspersed much larger tubercles. Granular scales finest over parietal region of head, becoming coarser over body**,** then larger, flatter and more polygonal on tail. On head dorsum (Fig. 11E), tubercles small and only slightly projecting, anteriorly commencing in the posterior crown area, becoming larger, more projecting and with a more conical apex over nape. Tubercles on body dorsum larger again (Fig. 12E) with a more longitudinally ovoid base and a low, weak median keel. Tubercles slightly larger over sacrum and large and somewhat flattened on tail base. Tubercles persist along tail, becoming lower and less differentiated until eventually losing their distinction by about the third dark band. Large tubercles on body dorsum separated by 2–5 smaller, granular scales. Tubercles on body arranged in about 20–24 (mean = 22.0, sd = 1.15, n = 16) roughly longitudinal rows. Dorsum of brachium with uniform, slightly imbricate scalation, larger tubercles very sparse to entirely absent; antebrachium with more imbricate slightly larger scales distally and over manus (Fig. 13E). Dorsum of thigh and crus with small juxtaposed granules and numerous, low tubercles (Fig. 13J), only dorsum of pes with imbricate scales.

Laterally, tubercles commence over temporal region (a few may be present in the postinfralabial area) where they are low and rounded and only slightly larger (Fig. 11J) than those of the head dorsum, then along nape and body, where they are smaller and noticeably less protuberant than those dorsally, and along tail, commencing on tail base as low, posteriorly deflected, conical scales, then rapidly losing differentiation within the first dark tail band (Fig. 14E).

Ventrally, gular scales small, rounded and juxtaposed, becoming larger, flat and more imbricate over body venter, from clavicular region. Ventral scales at midbody, between ventrolateral skin folds 35–45 (mean = 40.0, sd = 2.63, n = 16). Ventral scales on brachium and antebrachium like gular scales. On ventral surface of thighs, but not on crus or in precloacal region, an abrupt junction between enlarged imbricate scales and much smaller scales posteriorly, enlarged scales 58–66 between distal extent on each thigh (mean = 62.1, sd = 2.54, n = 16). Ventral scales of tail base like those of body, most of tail venter with a single median series of very broad scales about four times the width of adjacent ventrolateral scales.

Precloacal and femoral pores present in males, in a single continuous row, arching shallowly anteriorly in precloacal region. Pores 58–66 (mean = 62.5, sd = 2.62, n = 11), best developed in precloacal region where they are deep and transversely oriented, becoming much shallower, smaller and rounder distally under thigh. No pubic groove. About three large, blunt-tipped postcloacal spurs on ventrolateral surface of tail base, more projecting in adult males than in females.

Forelimbs and hindlimbs well-developed (FLL/SVL 15.0–16.6%, mean = 16.0%, sd = 0.37, n = 16; HLL/SVL 18.2–20.6%, mean = 19.0%, sd = 0.60, n = 16). Digits well-developed, reflected dorsally at proximal interphalangeal joint, and all bearing robust, strongly curved claws sheathed at the base by two scales. Subdigital lamellae expanded basally, beginning on pes over distal part of metatarsals and ending at point of reflection of toes, lamellae distal to this point not expanded. Lamellae under first toe 8–9 expanded (mean = 8.4, sd = 0.51, mode = 8 (56.3%)) + 10–12 narrow (mean = 10.8, sd = 0.66, mode = 11 (56.3%)), total 18–20 (mean = 19.3, sd = 0.68, mode = 19 (50.0%), n = 16). Lamellae under second toe 8–11 expanded (mean = 10.2, sd = 0.83, mode = 10 (50.0%)) + 12–14 narrow (mean = 12.6, sd = 0.63, mode = 12 (50.0%)), total 22–24 (mean = 22.8, sd = 0.68, mode = 23 (50.0%), n = 16). Lamellae under third toe 9–12 expanded (mean = 10.9, sd = 1.26, mode = 12 (50.0%)) + 13–16 narrow (mean = 14.0, sd = 0.97, mode = 13 (37.5%)), total 23–27 (mean = 24.9, sd = 1.09, mode = 25 (43.8%), n = 16). Lamellae under fourth toe 11–15 expanded (mean = 13.4, sd = 1.03, mode = 13 (37.5%)) + 12–16 narrow (mean = 14.3, sd = 1.35, mode = 15 (37.5%)), total 26–30 (mean = 27.8, sd = 1.18, mode = 28 (37.5%), n = 16). Lamellae under fifth toe 8–11 expanded (mean = 9.9, sd = 1.06, mode = 11 (37.5%)) + 13-19 narrow (mean = 14.7, sd = 1.82, modes 13, 15 (37.5%)), total 23–28 (mean = 24.6, sd = 1.31, mode = 24 (43.8%), n = 16). Relative lengths of digits on manus I<II<V<III<IV; on pes I<II<III=V<IV. Very slight traces of webbing between bases of fingers; weak webbing between bases of toes 2–3 and 3–4.

Tail a little longer than body (TL/SVL 130.5–132.7%, n = 2), narrow at base (TW/SVL 6.2–10.4%, mean = 7.4%, sd = 1.15, n = 16) and tapering evenly to a conical tip. Tail segments externally identifiable by straight scale junctions, segments about 7–9 scales long basally when counted to include tubercles. Cloacal sacs present in both sexes, larger in males, external orifices just posterior to vent, laterally.

Colour in preservative. Dorsal pale ground colour fawn. Head dorsum (Fig. 11E) somewhat darker but relatively unmarked, bordered posterolaterally by a narrow pale band. Pale nape zone bordered posteriorly by a U-shaped dark chocolate-coloured chevron on nape, widest vertebrally, and extending anteriorly over temporal region to eye, then visible as a narrowing, increasingly diffuse streak over the lores to the nostril; chevron deepest along vertebral region and with a small U-shaped dip on posterior midline. Second broad dark transverse dorsal band over shoulders, lateral margins extending anteroventrally in front of forelimbs. Three dark bands over trunk, extending lateroventrally with even width, but dissipating over flanks. One dark band over hips. Tail with dark bands over most of length, but these become increasingly diffuse near tip. When they can be counted to the distal end of tail, dark tail bands 11 (n = 2). On nape and body, the dark bands are markedly broader than the pale interspaces, and the posterior margin is strongly edged with darker pigment; each dark band fades progressively, often producing a water colour-like effect before merging with its anterior pale band. Dark tail bands (Fig. 14E) prominent chocolate brown and of similar width to body bands but much more distinct; more than twice as wide as pale interspaces. Pale interspaces of body unmarked.

Upper and lower lips (Fig. 11J) pale and unmottled. Dorsum of forelimbs and hindlimbs pale to mid brown, unpatterned.

Ventral surface of body cream but sometimes with diffuse brown pigment on abdomen. Ventral surface of tail generally dark but marked by pale blotches.

Description of holotype. The holotype of *C. pronarus* is a mature-sized male, with the following character states of those variable for the taxon: SVL 113 mm, AGL 51 mm, TL 150 mm, TW 7.1 mm, HL 32.3 mm, HW 21.8 mm, HD 11.1 mm, IN 4.0 mm, SL 12.8 mm, EN 9.7 mm, EYE 6.7 mm, EE 8.9 mm, EAR 2.1 mm, FLL 17.0 mm, HLL 21.0 mm, lamellae below digits I–V 9+11, 10+13, 12+15, 14+15, 10+15 respectively, supralabials 10, infralabials 12, rows of dorsal tubercles 22, transventral rows 43, femoroprecloacal scales 62, and dark tail bands 11.

Etymology. From the Greek πρό (pro = before) and ναρός (naros = flowing), alluding to the blending of the anterior edge of the dark body bands with the preceding pale interspaces.

Distribution. Known only from a small area of the McIlwraith Range, north-east of Coen, Queensland (Fig. 21). The three localities are within 22 km of each other, and all are at about 500 m asl. It is possible that the species occurs at higher elevations — the known localities represent accessible high points in the McIlwraith Range.

Conservation status. This species has a small known distribution that is unlikely to be much more extensive. We have no clear understanding of population size and under IUCN criteria regard it as Data Deficient. The large adult size and colourful pattern of this species may make it desirable for the illegal pet trade but it occurs in a remote, protected area that is largely inaccessible.

Comparison with other species (Table 6). *Cyrtodactylus pronarus* is morphologically and genetically most similar to *C. adorus*, differing from it genetically by 8.53% sequence divergence on average (Table 2). It is slightly larger than *C. adorus* (SVL males 104.5–126 mm *vs* 91.5–119 mm, females 113–132.7 mm *vs* 90.9–123 mm), has more numerous labial scales (supralabial modes 10 *vs* 9; infralabials 11–13 *vs* 10–11), the antebrachium lacks tubercles (small tubercles present in *C. adorus*); the dark nape band lacks an anterior vertebral extension (present in *C. adorus*); the dark body bands lack a sharply defined anterior edge, instead blending into the pale bands (sharply defined anterior and posterior margins to dark body bands in *C. adorus*), and the dark bands on the tail are much wider than the pale interspaces (pale tail bands about a third the width of the dark bands, while those of *C. adorus* are about half the width of the dark bands). The two species are at present geographically separated by 135 km, but the intervening ranges (northern McIlwraith Range, Table Range, Macrossan Range) and rock outcrops have been poorly surveyed for nocturnal reptiles.

Cyrtodactylus pronarus is more genetically distinct from *C. tuberculatus*, *C. mcdonaldi* and *C. hoskini*, with average sequence divergences between 16.72% and 17.72% (Table 2). Morphologically, it differs from *C. tuberculatus*, *C. mcdonaldi* and *C. hoskini* in having many more femoroprecloacal pores and enlarged femoroprecloacal scales (58–66 *vs* 48 or fewer for both characters). The hindlimbs are immaculate (*vs* mottled), the caudal dark bands are solid black (*vs* dark-edged with paler centres) and are much wider than the pale interspaces at the tail base (*vs* subequal width), and the lips are pale and immaculate, sharply contrasting with the brown face. In comparison to all three species, *C. pronarus* has much less developed tubercles, those that are present being smaller and less projecting than the other species, and the tubercles are greatly reduced on the tail, ceasing prior to the distal end of the first dark caudal band. In comparison to *C. mcdonaldi*, *C. pronarus* also has a continuous row of femoroprecloacal pores in males (*vs* broken into three segments). *Cyrtodactylus pronarus* also lacks vertebral extensions to the dark nape and body bands (present in *C. hoskini*), and has the anterior margins of the dark body bands diffusing into the pale interspaces (*vs* with dark anterior margins in *C. tuberculatus* and *C. hoskini*). It is also much larger than *C. hoskini* and *C. mcdonaldi* (SVL up to 133 mm *vs* 112 and 105 mm respectively) and a little larger than *C. tuberculatus* (maximum 120 mm).

It further differs from all other Australian *Cyrtodactylus* in usually having a small median scale (Fig. 10; probably a fragmented posterior portion of the mental) anteriorly separating the first pair of postmentals (a feature otherwise only seen in one individual of *C. adorus*).

In comparison to *C. robustus*, *C. pronarus* is smaller (maximum SVL 132 *vs* 161 mm), has lesser development of dorsal tubercles, has pale lips (*vs* mottled lips), the anterior margins of the dark body bands blend with the pale bands (*vs* anterior margins strongly defined by narrow dark then light band), lacks dark speckling on the venter and orange oral and cloacal mucosa, and has fewer dorsal tubercle rows (20–24 vs 24–30), femoroprecloacal pores and enlarged femoroprecloacal scales (58–66 *vs* 75 or more for both characters), and a generally narrower head (HW/HL 65–75%, mean = 69% *vs* 69–84%, mean = 77%).

In comparison to *C. klugei*, *C. pronarus* has more dark body bands over the trunk (three *vs* usually two), pale lips (*vs* brown posterior supralabials), anterior margins of dark body bands poorly defined (*vs* sharply defined), fewer transventral scales (35–45 *vs* 43–49), and fewer femoroprecloacal pores (58–66 *vs* 66–76) and enlarged femoroprecloacal scales (58–66 *vs* 69–77)

Natural history. Specimens collected at Peach Creek were living amongst large granite boulders along a drainage line in well-developed rainforest (Fig. 28). *Cyrtodactylus* have also been seen in similar habitat at Birthday Mountain. These are presumably also *C. pronarus* because of the close proximity of this locality to the McIlwraith Range.

Stomach contents of six individuals were reported by Covacevich *et al*. (1996; as *Cyrtodactylus louisiadensis*). Ten food items were reported: an unidentified centipede (Chilopoda), the spider *Heteropoda jugulans* (Heteropodidae), the scorpion *Lychas* sp. (Buthidae), unidentified moth (Lepidoptera), unidentified wasp (Vespidae), unidentified cricket (Gryllidae), and four roaches (two *Laxta* sp., two large *Calolampra* sp., Blaberidae).

FIGURE 28. Habitat of *Cyrtodactylus pronarus* at Peach Creek (Photo: A. Amey).

Key to Australian *Cyrtodactylus*

1	Scales in posteriormost enlarged femoroprecloacal row <50	2
-	Scales in posteriormost enlarged femoroprecloacal row >50	4
2	Dark body bands with darker anterior and posterior margins; femoroprecloacal pores in males in a continuous series from knee to knee	3
-	Dark body bands usually with only a darker posterior margin; femoroprecloacal pores in males in three patches, separated by several scales lacking pores	*C. mcdonaldi*
3.	Dark bars present ventrolaterally in the pale interspaces between the dark body bands, 38–44 ventral scale rows at midbody between ventrolateral skin folds	*C. hoskini*
-	No dark bars present ventrolaterally in the pale interspaces between the dark body bands, although a series of rounded spots may be present; 24–37 ventral scale rows at midbody between ventrolateral skin folds	*C. tuberculatus*
4.	Dark body bands with a sharply defined anterior margin; forelimb with small tubercles	*C. adorus*
-	Dark body bands without a sharply defined anterior margin; tubercles on forelimb sparse to absent	*C. pronarus*

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Appendix: Comparative material examined.

Cyrtodactylus salomonensis:

Bougainville I., Papua New Guinea: AM R11283–84, R11460, MCZ 65813–14, Buin (6º 50' S 155º 44' E); AM R12940–41, Bougainville; AM R111210, MCZ 72211–12, 72214, 72216–17, 73880, 73882, 75886, 80905, Kunua (5.76º S 154.72º E); MCZ 65565, Eivo area, Kieta (6.22º S 155.62º E); 65815, Boku (6.58º S 155.33º E); 89569, Topanas (5.58º S 155.03º E); 98760–61, Tinputz (5.55º S 155.00º E); 98762, Turiboiru (6.72º S 155.68º E); 98778, Mutahi (5.70º S 154.95º E); USNM 120883, Cape Torakina (6.25º S 155.03º E).

Kolombangara I., Solomon Islands: BPBM 3436, Pepele (8.05º S 156.9667º E).

New Georgia I., Solomon Islands: AM R134930–32, Mt Javi, 5 km N Tatutiva Village, Marovoa (8º 31' S 157º 52' E).

Russel Islands, Solomon Islands: AM R135311, Pavuvu I. (9º 03' S 159º 06' E); USNM 121386, Banika I. (9º 04' S 159º 11' E).

Guadalcanal I., Solomon Islands: AM R69569, Visale (9º 16' S 159º 42' E).

Choiseul I., Solomon Islands: AM R136309, Pavora River (6.77º S 156.54º E).

Santa Isabel I., Solomon Islands: SAM R56879–80, Kolopakisa (7º 36' S 158º 39' E) (types of *C. salomonensis*).

Malaita I., Solomon Islands: AM R87399, within a 3 mi. radius of Bitaama (8º 24' S 160º 36' E); R137204, R137210, R137212, R137214–19, Bsurata Village (8º 49' S 160º 49' E); BPBM 3484, Dala (8.58333º S 160.6667º E); MCZ 14467, Auki (8.76º S 160.70º E); 115584, 121244, Laugwata (8º 38' S 160º 40' E); USNM 313867, near Arabala Village (8.88º S 160.77º E).

Solomon Islands (no specific locality): QM J62631.

Cyrtodactylus epiroticus:

Morobe Province, Papua New Guinea: AMNH 66702, Lae (6.73º S 147.00º E); 92338–40, Oomsis Creek (6.65º S 146.80º E); 95174, Busu River, 8 mi. N Lae (6.62º S 147.00º E); 95648–51, Masba Creek (6.50º S 147.50º E); 95652, near Lae (6.73º S 147.00º E); 103240, Busu Logging Area (6.48º S 146.98º E); 103241, Munum Waters, 12 mi. W Lae (6.62º S 146.78º E); 104870, Garaina (7.88º S 147.13º E); BPBM 23977, Lae Botanic Gardens (6.73º S 147.00º E); 18653 (holotype), 18654, 9.7 km (air) NW Mt Shungol summit (Apele) (6.79065º S 146.66535º E); MCZ 49611, USNM 119230–31, Gusiko (6.42º S 147.83º E); MCZ 54244–45, Lambeang, Mongi River (6.61º S 147.59º E); 98926, Boana (6.42º S 146.82º E); USNM 159912–14, nr Kaluang River mouth, Finschafen (6.60º S 147.83º E).

Oro Province, Papua New Guinea: AM R9967, R9969, Mt Lamington (8.93º S 148.17º E); MCZ 140983, Sangara (8.73º S 148.22º E).

Milne Bay Province, Papua New Guinea: AMNH 74197, 74343, N slope of Mt Dayman, Maneau Range (9.75º S 149.23º E); 73995, 73997, 74001, 74112, Biniguni Village, Gwariu River (9.67º S 149.27º E); 74261, 74334, Peria Creek crossing, Kwagira River (9.65º S 149.32º E); 76725, Waikaiuna, Normanby I. (10.07º S 150.97º E); BPBM 2292, Sinaeada (10.325º S 150.338º E); 15434, south-east slope, Mt Pekopekowana (10.2806306º S 150.1721461º E); 16866, Camp 3, SE of Sewa Bay, Normanby I. (10.0416666º S 150.9817351º E); QM J2431, Cloudy Bay (10º 11' S 148º 41' E).

Papua New Guinea (no specific locality): QM J55367.

Cyrtodactylus klugei:

Sudest I., Milne Bay Province, Papua New Guinea: AMNH 76754, Rambuso (11.48º S 153.57º E); 76765, W slope Mt Riu (11.50º S 153.40º E); BPBM 19739 (holotype), 19740, Mt Riu, along Gesirava River, Camp 1 (11.49179º S 153.41261º E).

Cyrtodactylus louisiadensis:

Sudest I., Milne Bay Province, Papua New Guinea: BPBM 19741, Camp 1, Fence 2, Mt Rio (11.49179º S 153.41261º E) (neotype of *Gymnodactylus louisiadensis*); 19742, Mt Riu, along Gesirava River, Camp 1 (11.49179º S 153.41261º E): 19743, track up Mt Riu (11.49610º S 153.42413º E); 19744, Mt Riu, ridge N of Camp 1 (11.486413º S 153.414835º E); MCZ 156549, Rewa (11º 38' S 153º 42' E).

Cyrtodactylus robustus:

Rossel Island, Milne Bay Province, Papua New Guinea: AMNH 76734, Jinja (11.32º S 154.23º E); 76743, Abaleti (11.40º S 154.25º E); 89374, MCZ 153072, no other details; BPBM 19727, Camp 2, Fence 1, S slope Mt Rossel (11.35552º S 154.22459º E); 19728, 19731, 19737–38, along Rupu River (camp 3), N slope Mt Rossel (11.33537º S 154.2247º E);19729–30, along Wupu River, Mt Rossel (11.33805º S 154.22385º E); 19732, Gobubob, Mt Rossel (11.33535º S 154.22226º E); 19733, Vieli, Mt Rossel (11.33662º S 154.22362º E); 19734, vicinity of Cheme (11.32547º S 154.24023º E); 19735 (holotype), PNGNM 25169–70, along Wabu River, Mt Rossel (11.34194º S 154.21921º E); BPBM 19736, Wabu River area, Mt Rossel (11.3324275º S 154.2078754º E)

Cyrtodactylus tripartitus:

Misima Island, Milne Bay Province, Papua New Guinea: AM R124955, nr Bwagaoia village (10º 40' S 152º 50' E); R125263, no other details; AMNH 76812–13, N slope Mt Sisa (10.65º S 152.80º E); BPBM 16860–61, Liak, Nulia River (10.660789º S 152.6854395º E); 16862–63, Bwaga Bwaga Ridge camp (10.67395º S 152.68285º E); 16864 (holotype), 16865, east slope Oya Tau (10.6548913º S 152.6382783º E); SAM R62638, Misima Mine (10º 39' S 152º 47' E); R62639–42, coast below Misima mining camp administration area; R62643–44, rainforest adjacent ANFO shed, Misima Mine (10.66º S 152.79º E).